

SYSTEMATICS OF THE PEARLFISHES (PISCES: CARAPIDAE)

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ABSTRACT

A review of taxonomy, anatomy, ontogeny, ecology, and phylogeny of the ophidiiform family Carapidae was conducted using over 2,300 larval, juvenile and adult specimens. A cladistic classification based on swimbladder morphology, developmental and osteological characters of the vertebral column, fins, pectoral and pelvic girdles, gill arches, ethmoid, jaws, and habitat is presented. A total of 31 species (6 new names and one unnamed larval form) in seven genera are recognized in two subfamilies. A species previously assigned to *Echiodon* is made the type of a new monotypic genus. Species of the tribe Carapini are rearranged in the genera *Carapus* and *Encheliophis* largely on the basis of swimbladder morphology. Larvae are described for all genera except *Encheliophis* whose larvae are predicted to resemble those of *Carapus*. The vexillifer larva is unique to carapids. The tenuis juvenile stage, however, may be restricted to the ecologically specialized genera, especially *Carapus* and *Encheliophis*. The family is distributed over broad depth (0-2,000 m) and latitudinal (ca. 65°N to 60°S) ranges. In general taxa with more plesiomorphic characters are found in deeper water and higher latitudes while taxa with more apomorphic characters are found in tropical, shallow water. Highly specialized inquiline behavior is found in both tribes of the Carapinae and our phylogenetic hypothesis specifies independent acquisition of molluscan inquilinism, at least. Within the Carapini the genus with the most apomorphic characters, *Encheliophis*, is the most successful holothurian inquiline and the only holothurian inquiline in the Indo-Pacific. Species in its sister genus, *Carapus*, "switch" to non-holothurian primary hosts (asteroids or ascidians) when sympatric with *Encheliophis* in the Indo-Pacific. Atlantic species of *Carapus* retain holothurians as primary hosts. The distribution of sister species is usually allopatric and suggests that the presence or absence of inquiline behavior has no bearing on mode of speciation. Vicariance of sister species is frequently along depth or latitudinal gradients. There are no amphi-American sister species; the sister group of all eastern Pacific species or populations of carapids is either another Pacific form or an Atlantic-Pacific clade.

The pearlfishes (Carapidae) are a highly specialized family of shallow to moderately deep-dwelling fishes which occur in marine shelf and slope waters and which are most abundant and diverse in tropical seas. Although some species are free-living animals, the majority are inquilines within the body cavity of shallow-water invertebrate hosts such as bivalves (Pl. 1), holothurians (Pl. 2) and asteroids. These remarkable associations, as well as a unique early life history (see references below), account for the notoriety of the group (Trott, 1981).

Eggs, larvae and adults of the Mediterranean species, *Carapus acus* and *Echiodon dentatus*, attracted the attention of early European workers (Brunnich, 1768; Rafinesque, 1810; Oken, 1817; Risso, 1826; Cuvier, 1829) and constitute the first records of the family in the literature. From 1830-1880, many reports and descriptions of nominal forms (see Arnold, 1956 for a partial listing) resulted from collecting efforts in Atlantic and Pacific localities (notably, the works of Thompson, 1837; Muller, 1842; Kaup, 1856; Bleeker, 1856; Putnam, 1874; Jones, 1874). Initially, there was confusion over the status and relationships of larvae, and several nominal genera are based on larvae (*Porobranchus*—Kaup, 1860; *Vexillifer*—Gasco, 1870; *Helminthodes*—Gill, 1864). Although the identity of the larval form and the complex life history of pearlfish were first summarized by Emery (1880) for *Carapus acus*, subsequent workers continued to describe genera based



Plate 1. *Encheliophis dubius*, MCZ 72903 (Mollusc Dept.) encased as a blister pearl in the valve of *Pinctada mazatlanica*. Photo by M. Stiassny.

on larval morphology (*Pirellinus*—Whitley, 1928; *Leptofierasfer*—Meek and Hildebrand, 1928; *Disparichthys*—Herre, 1935).

The current taxonomic arrangement of the family is based primarily on the following contributions. Smith (1955a) summarized information on western Indian Ocean adult carapids, erected the genus *Onuxodon* and provided keys to the identification of four genera and 11 species (including four new species). Smith (1955b) erected the family Pyramodontidae to accommodate *Pyramodon* and, tentatively, *Snyderidia*. Arnold (1956) attempted the only complete review of the Carapidae (excluding the pyramodontines) on a worldwide basis, summarized information on natural history, behavior and early life history (primarily of *Carapus acus*), described some osteological variation, provided keys to three genera, two subgenera (*Onuxodon* and *Jordanicus* were treated as subgenera) and 22



Plate 2. *Carapus bermudensis* with its host, *Actinopyga agassizi*, collected off Bimini, Bahamas. Photo by M. Van Meter.

species (with figures and life history summaries), and discussed the status of three problematic types. Gosline (1960) provided a detailed description of salient anatomical features of adult *Snyderidia*, discussed the relationships of brotulids, ophidiids, carapids and pyramodontids and placed *Snyderidia* in the Pyramodontidae. Strasburg (1965) described the vexillifer larva of *Snyderidia* and firmly established the relationship between Pyramodontidae and Carapidae. Robins and Nielsen (1970) treated Pyramodontidae as a subfamily within Carapidae. Courtenay and McKittrick (1970) and Tyler (1970) re-erected the genus *Onuxodon*. Trott (1970) presented a systematic account of four genera and eight species from Atlantic and Pacific localities and discussed evolution of certain behaviors, such as parasitism in the family. Olney and Markle (1979), Markle and Olney (1980) and Govoni et al. (1984) described larval morphology in *Echiodon*, *Carapus*, *Pyramodon* and *Snyderidia*, establishing the vexillifer larva as a unique specialization of all Carapidae and reinforcing the subfamilial classification of Robins and Nielsen (1970). Gordon et al. (1984) summarized the status of knowledge of larval morphology in ophidiiform fishes and discussed intra- and inter-ordinal relationships. Finally, Williams and Shipp (1982), Markle et al. (1983) and Williams (1984a) recognized previously undescribed species of *Echiodon* and Williams (1983, 1984a, 1984b) provided a synopsis of subfamilies and genera.

Our interest in pearlfishes developed from an early attempt to identify larvae of an unnamed Atlantic species (Olney and Markle, 1979) and later success in using larval morphology to infer higher relationships (Markle and Olney, 1980; Gordon et al., 1984). During the course of these early studies, we began to recognize

Table 1. Abbreviations used in morphometric and meristic descriptions of larval, juvenile and adult pearlfishes

Morphometric		Meristic	
BD	body depth	A ₃₀	anal-fin rays to 31st vertebra
BI	bony interorbital distance	ARDO	anal-fin rays anterior to dorsal-fin origin
ED	horizontal diameter of pigmented eye	D ₃₀	dorsal-fin rays to 31st vertebra
HD	head depth	DRAO	dorsal-fin rays to anal origin
HL	head length	MAO	myomeres to anal-fin origin
HW	head width	MDO	myomeres to dorsal-fin origin
LJL	lower jaw length	MVO	myomeres to vexillum origin
LTP	length to pectoral-fin base	P ₁	pectoral-fin rays
N	number of specimens	VAO	vertebrae to anal-fin origin
NL	notochord length	VDO	vertebrae to dorsal-fin origin
PAL	preanal length	VPB	vertebrae under predorsal bone
PDL	predorsal length	VVO	vertebrae to vexillum origin
PVL	preexillum length		
PL	pectoral-fin length		
SL	standard length		
SNL	snout length		
STA	snout to anus		
SD	standard deviation		
TL	total length		
UJL	upper jaw length		
VL	vexillum length		
\bar{x}	mean		

the inadequacy of existing classifications, the wealth of morphological data available for analysis and the need for a comprehensive revision of the family. The purpose of our study was to incorporate information from anatomy, ontogeny, and habitat in a cladistic analysis of the intrarelationships of the Carapidae and to compare this phylogeny to Trott's (1970) existing hypothesis of relationships based on behavior and ecology.

METHODS

Sources of Material.—Standard acronyms for resource collections follow Leviton et al. (1985) and Leviton and Gibbs (1988) except DAFS is used for Dunstaffnage Marine Lab, Oban, Scotland. Over 2,300 larval, juvenile and adult specimens (1,453 lots) were examined during the course of this study. Some material was donated (see Acknowledgments) and has been deposited in collections at AMNH, OS, USNM and VIMS. Most specimens examined were loaned from the following institutions: AMS, ARC, AMNH, BMNH, BPBM, CAS, CAS-SU, FAKU, GCRL, GMBL, HUMZ, ISH, LACM, MCZ, MMF, MNHN, MZUSP, NMNZ, OS, QM, ROM, RUSI, SIO, UF, USNM, VIMS, WAM and ZMUC. A complete listing (in dBASE III Plus files: Ashton-Tate, registered trademark) of data including host and locality information for all specimens is available on floppy disk from the authors as well as on deposit at the USNM.

Abbreviations, Terms and Definitions.—Abbreviations used in morphometric, meristic and osteological descriptions of larval, juvenile and adult pearlfishes are presented in Tables 1–2. Counts follow Olney and Markle (1979), Markle and Olney (1980), and Markle et al. (1983) with the following emendations: DRAO (dorsal fin rays anterior to a vertical through the anal fin origin) and ARDO (anal fin rays anterior to a vertical through the dorsal fin origin); except in cleared and stained material, pectoral-fin counts were made on specimens by careful dissection of epidermis and musculature covering the radials; vertebrae under predorsal bone (VPB) are reported as minimum and maximum values when the bone is over more than one centrum. Some measurements are straight line dimensions, i.e., verticals were not used in measurements of head length (HL), preanal length (PAL), predorsal length (PDL), preexillum length (PVL), standard length (SL), total length (TL) or snout to anus length (STA). Body depth (BD) was measured as a vertical through the anal-fin origin and head depth (HD) as a vertical through the angular. Snout length (SNL) was measured as the distance between the tip of the snout

Table 2. Abbreviations used in osteological descriptions of larval, juvenile and adult pearlfishes

ACCR	accessory pectoral-fin radials	INAR	interarcual element
ANGL	angular	INHY	interhyal
ANUS	anus	INOP	interopercle
ARTC	articular	LATE	lateral ethmoid
BAHY	basihyal	LIGA	ligament
BAS1-4	basibranchial of arch 1-4	MAXL	maxilla
BAPH	basisphenoid	MESO	mesopterygoid
BRRY	brachiotegial ray	META	metapterygoid
BSOC	basioccipital	MPR	modified proximal radial
CLEI	cleithrum	NA	neural arch
CNT-1	first centrum	OPER	opercle
CORA	coracoid	PALA	palatine
CORM	coronomeckelian	PARA	parahypural
CRT1-5	ceratobranchial of arch 1-5	PFRY	pectoral-fin ray
CTST	ceratohyal strut	PHR1-4	pharyngobranchial of arch 1-4
CTHY	ceratohyal	PMFL	premaxillary flange
DENT	dentary	PMAX	premaxilla
DHYP	dorsal hypohyal	PMXC	premaxillary cartilage
DIAS	diastema	POCL	postcleithra
EPI1-4	epibranchial of arch 1-4	PROP	preopercle
ETMD	ethmoid	PRRD	proximal pectoral-fin radials
EPHY	epihyal	QUAD	quadrate
EXOC	exoccipital	SBOP	subopercle
FAP	first anal pterygiophore	SCAP	scapula
FDIR	first distal radial	SWBL	swimbladder
FDP	first dorsal pterygiophore	SYMP	symplectic
FNS	first neural spine	TMXC	transitory maxillary cartilages
FRNT	frontal	UR12	ural centra 1 and 2
FRNF	frontal flange	URHY	urohyal
HY12	hypurals 1 and 2	VHYP	ventral hypohyal
HY35	hypurals 3-5	VE	vexillum
HYOM	hyomandibular	VPRC	ventral processes of coracoid
HYP1-3	hypobranchial of arch 1-3	VOMR	vomer
HYST	hypohyal strut		

and the anterior margin of the pigmented eye. All measurements were recorded in mm (usually with three significant digits) and reported as such for type material. Measurements (except HL and TL) for other specimens are reported as a ratio to HL. We appreciate the problems associated with the use of ratios, especially over the size extremes we have studied; accordingly, we separate results of larval and adult specimens. There are dramatic allometric changes in carapid development, such as the relationship of HL to TL documented herein. Unfortunately, sample sizes much greater than those available to us are needed to describe such morphological changes. We, therefore, have used morphometry as a gross identification tool.

The terms "transverse process" and "ribs" of Markle et al. (1983) are equivocal and are given particular attention in the section Characters and Polarity. In our descriptions, we now follow Markle (1989) and refer to the structures on the first two centra as epipleurals, to the expanded structures on subsequent centra as parapophyses, and to the structures attached to parapophyses in pyramodontines as pleural "ribs."

Phylogenetic Reconstruction and Outgroups.—Our approach to classification is cladistic, following the tenets of Hennig (1966). We use outgroup comparison (Watrous and Wheeler, 1981; Maddison et al., 1984) and, when possible, ontogeny plus outgroup comparison (O'Grady, 1985). Carapids present a problem in outgroup analysis since their relationship to other ophidiiform groups is poorly understood. According to Maddison et al. (1984) "the basal members of a heterogenous outgroup have the most influence on the ancestral state assessment not because they are primitive in most characters and thus should have primitive states of the characters of interest, but because they will have the most influence on the most parsimonious assignment to the outgroup node." The basal member or sister group of all other ophidiiforms is unknown, as is the sister group of carapids. Thus, the character states at the carapid family node likely will be equivocal. We have used, therefore, what we feel are relatively

primitive ophidiiforms, *Brotula* (the ophidiid subfamily Brotulinae) and *Brotulataenia* (the ophidiid subfamily Brotulataeniinae) as well as several other ophidiids and bythitids. Our initial approach has been to demonstrate monophyly of the family Carapidae and secondly to ascertain which characters show obvious variation within the family. In the few instances of family synapomorphies for which there are no corresponding ophidiiform conditions (e.g., the vexillum), morphological variability within the family was analyzed using subfamily outgroups. Accordingly, pyramodontines become the outgroup for carapines and vice versa. In these cases, if the state under consideration is invariable in the outgroup, the plesiomorphic condition is that state found in both subfamilies. For example, all known pyramodontine larvae possess a vexillum supported by a simple vexillar radial. Since carapine larvae possess both simple and compound vexillar radials (see Ontogeny section for details), the simple condition is considered primitive.

In our analysis, the distribution of four adult character states (pelvic fin loss, > 15 PCV, a rounded ethmoid and fang-like teeth at the symphysis) yields four instances of equally parsimonious hypotheses at the family node. We acknowledge these alternatives in the sections that follow (Characters and Polarity, Relationships) and consistently choose hypotheses that show parallel trends between subgroups (subfamilies). For example, we hypothesize independent loss of pelvic fins in both carapid subfamilies rather than a single loss coupled to an atavistic reversal. All probable sister groups and one carapid genus (*Pyramodon*) have pelvic fins, so the loss is derived. Alternatively, all carapines and one pyramodontine (*Snyderidia*) lack pelvic fins, so, by subfamily outgroup comparison, the loss could be considered primitive and the reversal derived. Both approaches are equally parsimonious but the former is based on an estimation of the carapid ancestral node from the family outgroup while the latter estimates the carapid ancestral node from within the family. We try to solve character polarities simultaneously with the outgroups, as well as within the ingroup, and in this example take the former approach. This choice has the added advantage that it treats two independent losses conceptually as simpler than one loss coupled with *de novo* reacquisition (see Relationships section).

Continuously variable meristic characters frequently show derived trends when subjected to outgroup comparison. They are notoriously difficult to polarize because cladistics demands that the individual, not the taxon, be the bearer of phylogenetic information (Hennig, 1966). Any cut-off point in a variable distribution is necessarily arbitrary and members of a single species can, therefore, fall on either side of such a cut-off point, thus producing the meaningless condition of possessing both apomorphic and plesiomorphic states of a character. In an attempt to avoid this situation, we identify character states in three continuous variables (PCV, VAO, and P_1) by inspecting the data for discontinuities in distribution. Occasionally, we encountered slight overlap in the outer limits of these variables. For example, we identified a trend of anterior movement of the anal-fin origin culminating in low VAO values in some species of Carapini and consider a VAO count equal to or less than 8 to be a derived state in all carapines and *Pyramodon ventralis* (see Characters and Polarity section). Although the lower limit of VAO in *Snyderidia canina* and *P. punctatus* overlapped this character, only one specimen of each species possessed a count of VAO = 8.

We use ontogeny both as a source of characters and as a tool to determine homology. For example, ontogenetic resorption of structures and different ontogenies are used, respectively, to indicate lack of homology between character states (see below). As a character, the primary diagnostic feature of carapid larvae, the vexillum, is, in our view, a significant carapid synapomorphy.

A cladogram was constructed manually and compared with cladograms produced using the MULPARS branch-swapping option of D. Swofford's software package, Phylogenetic Analysis Using Parsimony (PAUP), version 2.4. Data matrix inputs are available from the authors.

Species Problems.—A number of populations in several genera were difficult to resolve taxonomically. Of eight cases (Table 3), two were resolved by either retaining existing nomenclature (*Echiodon drummondi*, *Ec. dentatus*) or re-establishing available names (*Onuxodon fowleri*), and six remain essentially unresolved. All eight cases shared several characteristics, namely: (1) available distribution data suggested or confirmed allopatry and (2) morphometric (especially ED and maximum HL, TL), and/or meristic variability (occasionally clinal trends in counts), and/or pigment variability suggested or confirmed morphological divergence. Details of these specific cases as well as arguments supporting their disposition are presented in individual sections of the following species accounts. Our intention here is to point out those taxonomic decisions that were difficult, to justify them on the basis of sample size, and to underscore these identification problems for consideration by future workers. It is important to point out that because of the probability of teleplanktonic larvae for all carapid species, we have avoided the use of apparent geographic disjunctions as a "character" in making taxonomic decisions.

In the six cases of unresolved taxonomic status (Table 3), very small sample sizes (3–15 specimens) resulted either in synonymy of several taxa (*Carapus acus*, *C. cuspis*, *C. birpex*; *Snyderidia canina*, *S. bothrops*; *Eurypleuron owasianum*, *Ec. cinereus*; *Echiodon coheni*, *Ec. anchipterus*) or failure to recognize new forms (Brazilian *Echiodon* or Gulf of Aden *Encheliophis*). We do not imply that larger sample sizes would automatically force recognition of separate taxa in these examples; however, large sample sizes (40–92 specimens) increased our confidence in the evaluation of *Onuxodon* and eastern

Table 3. Summary of species identification problems and their disposition

Populations	Evidence of speciation	Sample size	Disposition
<i>Echiodon</i> : North Sea vs. Mediterranean	1. morphometry including ED, maximum HL, maximum TL	moderately large, approximately 40 specimens	separate species: <i>Ec. drummondi</i> , <i>Ec. dentatus</i>
<i>Echiodon</i> : Somali vs. Phillippines	2. allopatry 1. allopatry	small, 3 specimens	unresolved, conspecific with <i>Ec. coheni</i>
<i>Carapus acus</i> : Eastern temperate and South Atlantic vs. Mediterranean	2. pectoral-fin counts 1. morphometry especially, ED, maximum HL and TL 2. pigment, meristic variability 3. allopatry?	small, approximately 12 specimens	unresolved, conspecific with <i>C. acus</i>
<i>Echiodon dawsoni</i> : Western North Atlantic, Caribbean vs. South Atlantic	1. esophagus and anterior stomach pigment 2. allopatry?	small, 3 specimens two of which are damaged	unresolved, conspecific with <i>Ec. dawsoni</i>
<i>Encheliophis vermicularis</i> : Eastern Pacific and Indo-west Pacific vs. Gulf of Aden	1. allopatry 2. morphometry including maximum HL and Maximum TL 3. some clinal variation in meristics	small, 3 specimens from Gulf of Aden	unresolved, conspecific with <i>En. vermicularis</i>
<i>Onuxodon</i> : Western Australia vs. Pacific and Indian Ocean	1. growth patterns 2. meristics, especially PCV 3. allopatry?	large, approximately 92 specimens	separate species: <i>O. fowleri</i> and <i>O. margaritiferae</i>
<i>Snyderidia</i> : Atlantic vs. Indian and Pacific	1. allopatry	small, 13 specimens	unresolved, conspecific with <i>S. canina</i>
<i>Eurypleuron</i> : Japan vs. other Pacific localities	1. allopatry 2. stomach color, meristics	small, 14 specimens	unresolved, conspecific with <i>Eu. owasianum</i>

Atlantic *Echiodon*. In three instances (*Echiodon pukaki*, *Ec. pegasus* and *Carapus sluiteri*), taxonomic decisions could be made in spite of small sample size. These decisions were based on extreme meristic disparity in *Ec. pukaki* and *Ec. pegasus*, and anatomical, meristic and host-specificity disparity in *C. sluiteri*. Although large sample sizes increased our confidence in evaluation of certain characters, the tendency in these data for significantly different means or slopes but overlapping extremes (e.g., eye diameter in *Ec. dentatus* and *Ec. drummondi*; precaudal vertebrae in species of *Onuxodon*) forced some degree of subjectivity. We stress the need for additional material and study.

CLASSIFICATION OF THE CARAPIDAE

To facilitate discussion of results, we initially present our classification as a framework for the remainder of the paper:

Carapidae Jordan and Fowler, 1902

Pyramodontinae Smith, 1955b

Snyderidia Gilbert, 1905

Snyderidia canina Gilbert, 1905

Pyramodon Smith and Radcliffe, 1913

Pyramodon lindas new species

Pyramodon parini new species

Pyramodon ventralis Smith and Radcliffe, 1913

Pyramodon punctatus (Regan, 1914)

Carapinae Jordan and Fowler, 1902

Echiodontini new name

Eurypleuron new genus (abbreviated *Eu.* in text)

Eurypleuron owasianum (Matsubara, 1953)

Echiodon Thompson, 1837 (abbreviated *Ec.* in text)

Echiodon unnamed larva

Echiodon pukaki new species

Echiodon coheni Williams, 1984a

Echiodon exsilium Rosenblatt, 1961

Echiodon dawsoni Williams and Shipp, 1982

Echiodon neotes new species

Echiodon drummondi Thompson, 1837

Echiodon dentatus (Cuvier, 1829)

Echiodon pegasus new species

Echiodon cryomargarites Markle, Williams, and Olney, 1983

Echiodon rendahli (Whitley, 1941)

Onuxodon Smith, 1955a

Onuxodon parvibrachium (Fowler, 1927)

Onuxodon margaritiferae (Rendall, 1921)

Onuxodon fowleri (Smith, 1955a)

Carapini Jordan and Fowler, 1902

Carapus Rafinesque, 1810

Carapus acus (Brunnich, 1768)

Carapus bermudensis (Jones, 1874)

Carapus sluiteri (Weber, 1913)

Carapus mourlani (Petit, 1934)

Encheliophis Muller, 1842 (abbreviated *En.* in text)

Encheliophis dubius (Putnam, 1874)

Encheliophis homei (Richardson, 1844)

Encheliophis boraborensis (Kaup, 1856)

Encheliophis sagamianus Tanaka, 1908

Encheliophis gracilis (Bleeker, 1856)

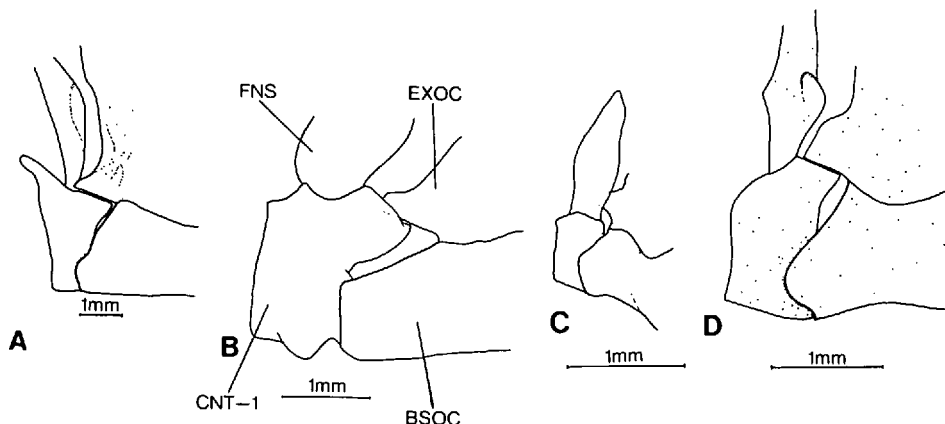


Figure 1. The first vertebral centrum and its anterior facets in A) *Pyramodon parini* USNM 298306, B) *Eurypleuron owasianum* AMS 16574-003, C) *Onuxodon fowleri* OS 11059, D) *Encheliophis homei*, USNM uncat.

Encheliophis vermiops new species

Encheliophis vermicularis (Muller, 1842)

CHARACTERS AND POLARITY

Characters used in our cladograms are numbered and listed in boldface in the following sections.

Osteology

Vertebral Column (Figs. 1–8).—Among ophidiiforms there are many specializations involving the skull, swimbladder, ribs and vertebrae, and an assortment of muscles and ligaments (Rose, 1961; Svetovidov, 1961; Courtenay and McKittrick, 1970; Courtenay, 1971). Two functional explanations have been suggested for these specializations: (1) that they provide a mechanism to adjust the body's center of gravity to facilitate "tail standing" or tail entry into substrates or other organisms (Svetovidov, 1961); or (2) that they are associated with sound production (Courtenay and McKittrick, 1970). In some ophidiids these specializations are sexually dimorphic (Rose, 1961), whereas in carapids, sexual dimorphism has not been previously documented (Courtenay and McKittrick, 1970). We have observed sexual dimorphic specializations in some carapids and discuss these in the *Echiodon drummondi*, *Ec. dentatus*, *Ec. rendahli* and *Eurypleuron owasianum* sections below.

The first vertebral centrum in ophidiiforms has three anterior facets (Rose 1961: fig. 2-*Ophidion*; Courtenay and McKittrick, 1970: figs. 1, 2-*Carapus* and *Onuxodon*). The ventral facet is slightly rounded and fits in a socket formed by the basioccipital. It appears to allow some lateral movement of the skull relative to the vertebral column and varies little in the material examined. Laterally the paired dorsal facets each meet a process of the exoccipital in *Brotula*, the other ophidiids and *Pyramodon* (Fig. 1A). In *Snyderidia* and the Carapini the joint is little modified (Fig. 1D). In echiodontines the exoccipital process appears spur-like and either sits on a modified first centrum (*Echiodon* and *Eurypleuron*, Fig. 1B) or reaches towards and sometimes into the first neural arch (*Onuxodon*, Fig. 1C). The lack of paired, dorsal, articular facets on the first centrum is a synapo-

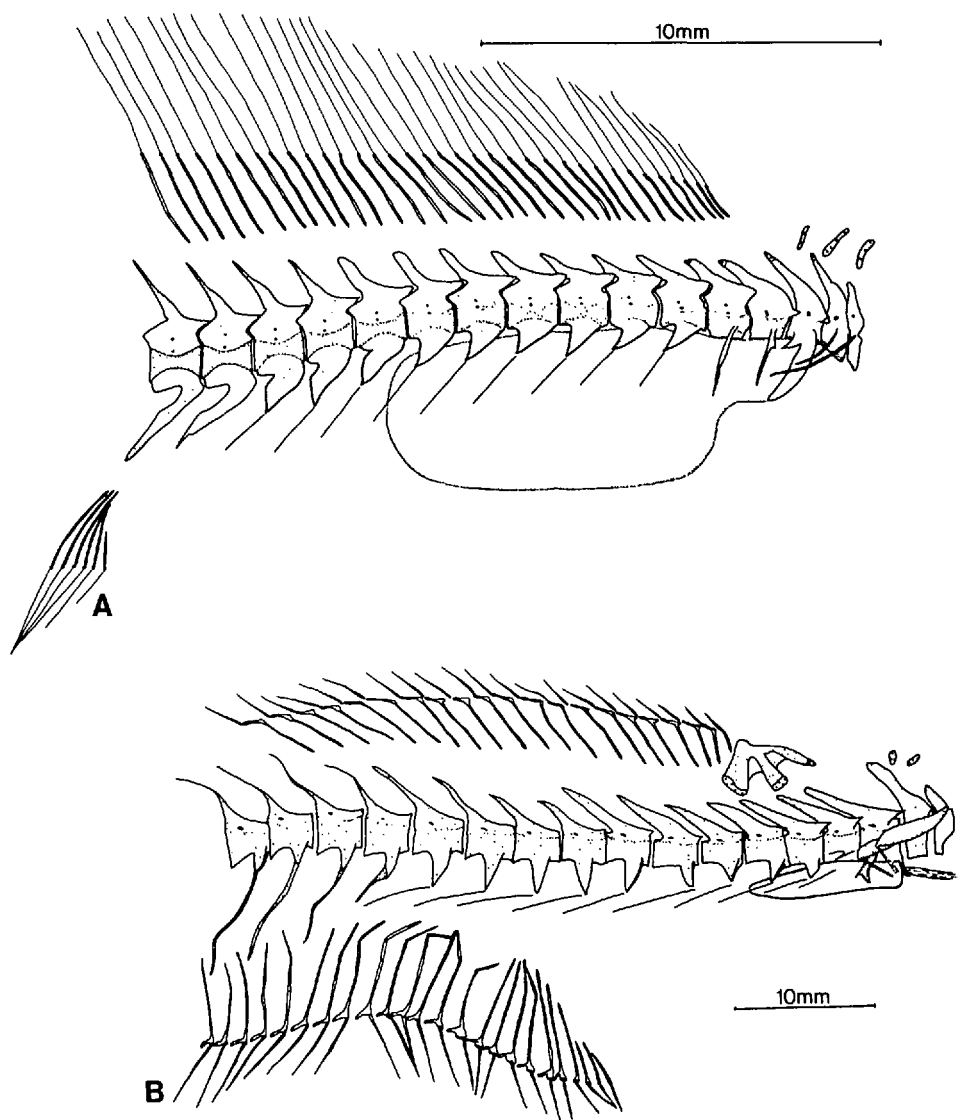


Figure 2. Anterior axial skeleton of A) *Brotula multibarbata* AMS uncat., B) *Snyderidia canina* USNM 214033.

morphy of the Echiodontini (1). In *Echiodon* and *Eurypleuron*, the highly modified first centrum that meets the exoccipital process in an unpaired articulation is a synapomorphy (2). The complete lack of any contact between the exoccipital process and first centrum and the extension of the process into the space of the first neural arch is a synapomorphy in *Onuxodon* (3).

The first neural spine in ophiidiiforms is always reduced relative to the second. It may be highly modified as in *Ophidion* (including *Rissola*, Courtenay, 1971) or *Otophidium* (UF34270). In carapids there is little modification. The presumed primitive state, found in *Brotula*, *Brotulataenia* (Cohen, 1974), *Pyramodon* and *Snyderidia*, shows a reduced spine that is inclined posteriad as are all subsequent

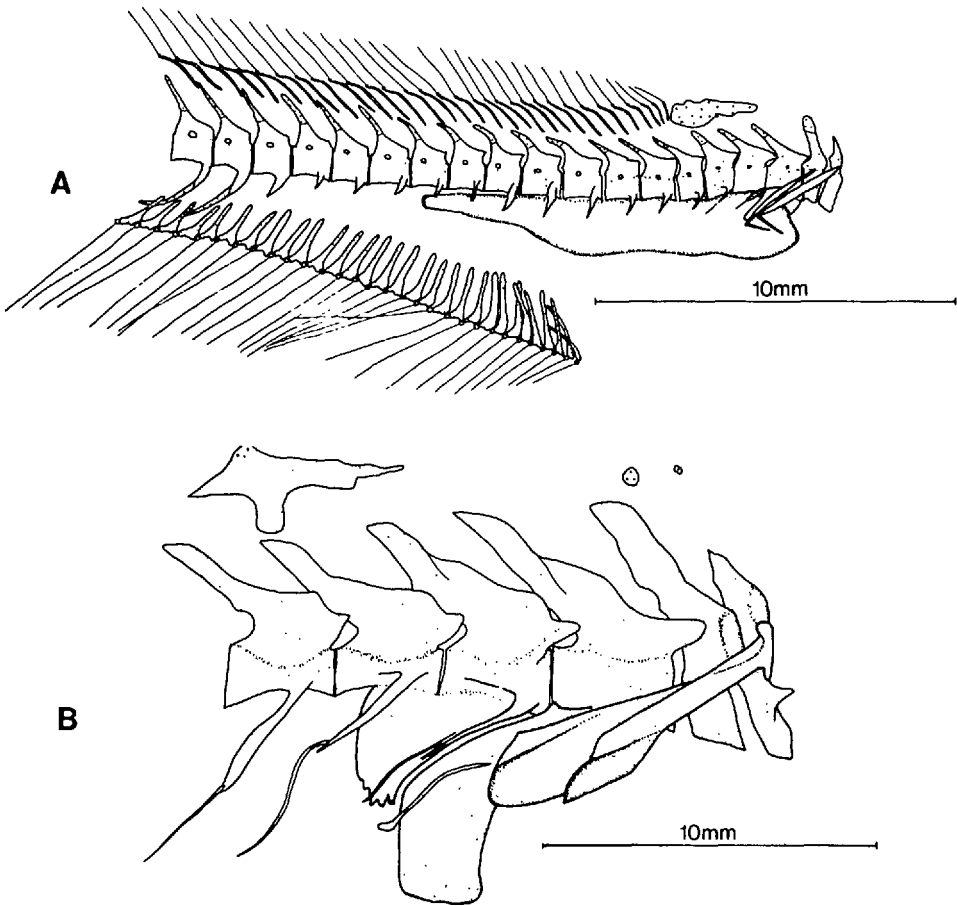


Figure 3. Anterior axial skeleton of A) *Pyramodon punctatus* USNM 219341, B) *P. parini* USNM 298306.

neural spines (Figs. 2, 3). In the Carapinae, the inclination of the 1st neural spine is vertical or anteriad (Figs. 4–6), a condition interpreted as synapomorphic (4). Immediately posterior and dorsal to the first neural spine are one to three supraneural cartilages. These structures are found in *Brotula* (Fig. 2A), *Dicrolene*, and *Lepophidium* but not in the other ophidiids. They are also present in one *Pyramodon* (*parini*), *Snyderidia*, *Carapus*, and three species of *Encheliophis* (*homei*, *parvipinnis* and variably in *vermicularis*) (Figs. 2, 3, 6). Loss of supraneural cartilages is an equivocal character at the family node as well as the subfamily node and little information can be attached to it. Clearly, the loss has been independent in adults of several carapid clades as well as some ophidiids.

A predorsal bone, the remnant of the vexillar pterygiophore and not a supraneural homologue, is present in all adult carapids except the Carapini (Figs. 2–6) where it is resorbed ontogenetically. It is not found in *Brotula* (Fig. 2) or other ophidiiforms. Cohen (1974) illustrates, and we confirm, an interesting, flattened first dorsal pterygiophore in *Brotulataenia* that resembles the predorsal bone of *Snyderidia* and *Pyramodon*. The modified first dorsal pterygiophore of *Brotulataenia* may not be homologous with carapid predorsals, however, since the larva

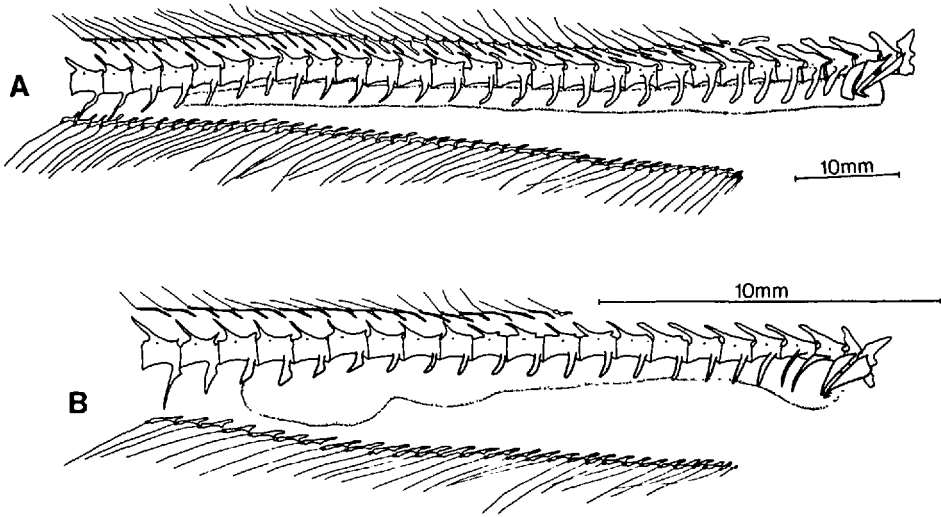


Figure 4. Anterior axial skeleton of A) *Echiodon drummondi* DAFS uncat., B) *Ec. dawsoni* UF 30886.

identified as *Brotulataenia* does not possess a vexillum (Aboussouan, 1980). We have not been able to examine Aboussouan's (1980) larva and cannot confirm his identification. Meristic values and the position of the first anal-ray pterygiophore in Aboussouan's larva match data reported for adult *Brotulataenia crassa* by Cohen, 1974. However, the morphology, arrangement and position of anterior dorsal pterygiophores in the larva do not agree well with Cohen's (1974: 131) illustration of adult material.

Williams (1984a) reported that a predorsal bone was absent in adults of some

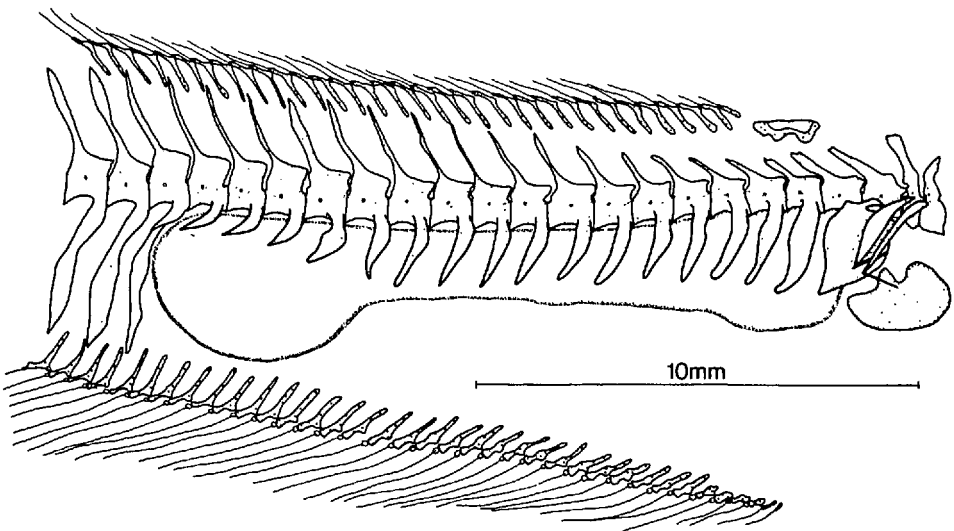


Figure 5. Anterior axial skeleton of *Onuxodon fowleri* OS 11059.

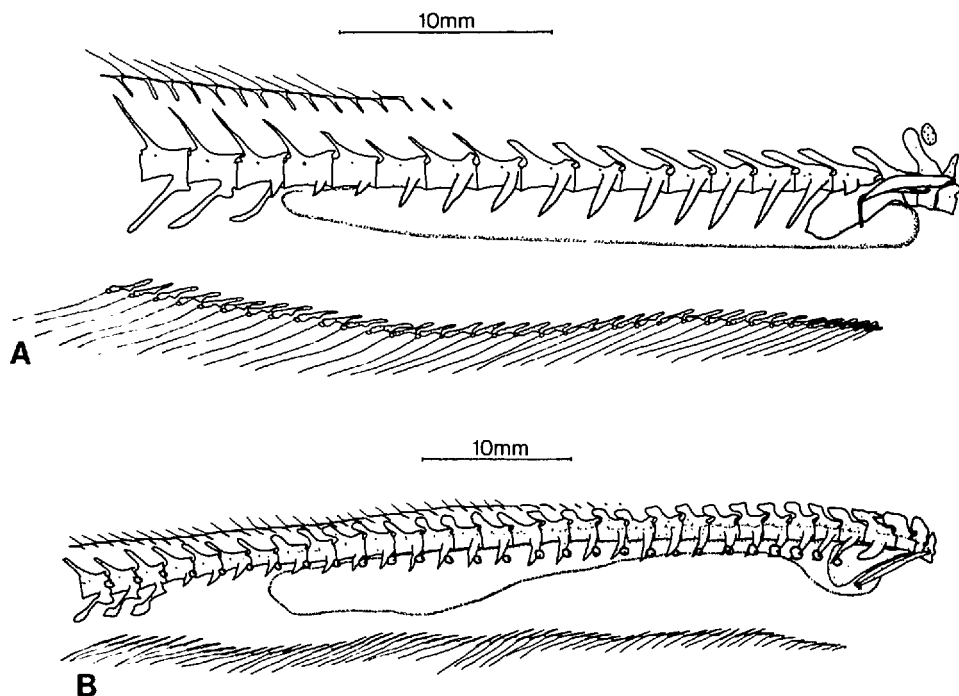


Figure 6. Anterior axial skeleton of A) *Encheliophis homei* OS 12480 B) *En. gracilis* UF 34265.

species of *Echiodon* (Fig. 4) but this observation is inconsistent with our interpretation. The problem is one of semantics as well as Williams' (1984a) lack of an ontogenetic perspective. An unrestricted use of the term "predorsal bone" would falsely equate conditions in the Carapini and some *Echiodon* (see above). In those species in which Williams (1984a) found no predorsal bone, the vexillar radial is a compound structure, supporting the first "adult" dorsal-fin ray as well as the vexillum (Olney and Markle, 1979; Gordon et al., 1984; see Ontogeny section). When the larval vexillum is lost, its radial remains as the radial supporting the first "adult" dorsal-fin ray. The homologue of the "predorsal bone" is, therefore, present in all *Echiodon*.

The retractor dorsalis muscle originates on the third centrum in carapids and the other ophidiiforms examined. In *Pyramodon* and *Snyderidia* there is a well developed facet which receives this muscle (Figs. 2B, 3A) on the ventral surface of the third centrum that we consider a synapomorphy of pyramodontines (5).

Pleural ribs are found in *Brotula*, the ophidiids, *Pyramodon* and *Snyderidia* (Figs. 2, 3). Our interpretation of these structures is based on the serial relationship seen in *Pyramodon parini* (Fig. 3B). We interpret the anterior "ribs" as epipleurals, the expanded processes as parapophyses, and, thus, the distal articulation of free elements on parapophyses of the third and subsequent centra in Figure 3B indicates that those elements are pleural ribs. Markle (1989) gives additional reasons for this interpretation in paracanthopterygians generally. The loss of pleural ribs in the Carapinae (Figs. 4–6) is a synapomorphy (6).

Ligaments connect the tips of the first two epipleural ribs to the anterior section of the swimbladder, to each other, to the first pleural rib (located on the third centrum), and/or (in *Onuxodon*) to the rocker bone (Figs. 2–6). The epipleural

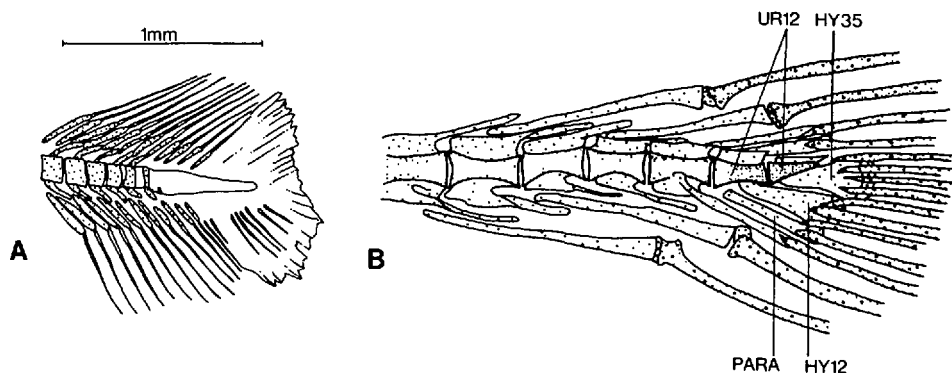


Figure 7. Development of the caudal fin in *Brotula multibarbata* A) AMS uncat., 12.6 mm NL, B) AMS uncat., 53.8 mm SL.

ribs are always movable. Ligaments are missing in *Brotula* (Fig. 2A) but present in the other ophidiids examined (see also Rose 1961). A compound swimbladder ligament, originating on the combined tips of the epipleural ribs, is a synapomorphy for the Carapini (7) (Fig. 6, Courtenay and McKittrick, 1970).

The first parapophysis (located on the third centrum) is greatly expanded posteriorly and lies underneath the fourth or fourth and fifth parapophyses (Fig. 6) in the Carapini, a synapomorphy (8). The loss or fusion of the fourth parapophyses to the third in *Onuxodon* (Fig. 5) is a synapomorphy (9). In *Eurypleuron owasianum* the fourth appears to be free and movable, at least in our cleared and stained specimen (AMS 16574-003), and in males there are greatly expanded plate-like parapophyses on centra 5 to 18–22, an autapomorphy (10) (Fig. 59).

The number of precaudal vertebrae is about 15 in *Brotula* (Fig. 2A), *Brotula-taenia* (Cohen, 1974), bythiids, and the ophidiids examined. Precaudal vertebral counts of 14–15 are also found in two pyramodontines, *Pyramodon ventralis* and *Snyderidia canina*. We interpret increases in precaudal vertebral numbers as the derived condition. Following our protocol for meristic characters, we established three derived states for this character as >15 (derived state 11), >25 (derived state 12), and >32 (derived state 13) precaudal vertebrae (Table 4). Increases in PCV occur independently in pyramodontines and carapines. With respect to character 11 (>15 PCV), we acknowledge that it is equally parsimonious to hypothesize a single acquisition of this character as a family synapomorphy and atavistic reversal in *Snyderidia* and *P. ventralis*. We hypothesize independent acquisition of character 12 (PCV >25) in *Encheliophis gracilis* and some *Echiodon* coupled with a reversal in four *Echiodon* species (unnamed, *dawsoni*, *exsilium*, and *coheni*).

Spatulate haemal spines are found in all *Carapus* and *Encheliophis* (Fig. 6B) except *C. bermudensis* and *En. homei* (Fig. 6A). These broad-tipped spines are not found in any outgroup and have evolved independently (14) in both lineages of the Carapini. The alternative hypothesis of atavistic reversal of this character in *C. bermudensis* and *En. homei* is less parsimonious.

Caudal Skeleton.—Development of the caudal skeleton of *Brotula* is shown in Figure 7. Most pearlfish specimens lack a caudal skeleton. However, apparently complete (as opposed to regenerated) caudal skeletons have been illustrated for *Echiodon dentatus* and *C. acus* (Ryder, 1886: pl. 7, figs. 3, 4), and we have seen them in *Ec. pegasus*, *P. parini* (Fig. 8) and a larval *Carapus* (Govoni et al., 1984: fig. 4). In our cleared and stained adult material only *P. parini* has a caudal skeleton.

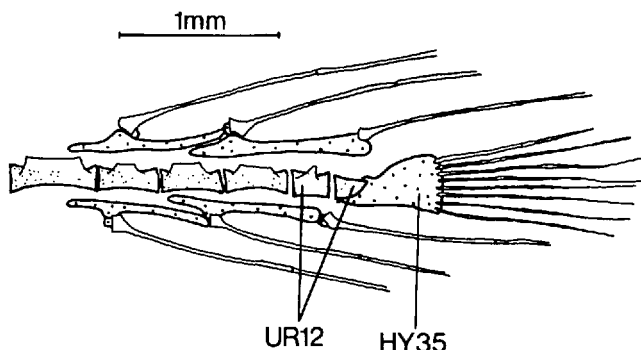


Figure 8. Caudal skeleton of *Pyramodon parini* USNM 298306.

Neural or haemal spines, haemal arches, epurals, parahypural and uroneurals are absent (Fig. 8). There are eight caudal rays and a single, fused hypural. The widespread absence of caudal fins in carapids may be due to ontogenetic suppression or mechanical loss. There does not appear to be any phylogenetic information in the structure.

Dorsal and Anal Fins (see also Ontogeny, below).—Dorsal- and anal-fin pterygiophores are thin and elongate in *Brotula*, *Brotulataenia* (Cohen, 1974), the ophidiids, and pyramodontines (Figs. 2, 3). Salient features of the anal-fin pterygiophores of *Snyderidia* are their frailty, frequently manifested as breaks, some of which seem healed (Fig. 2B) and their somewhat random position. Williams (1983) misinterpreted this latter condition as the presence of a visceral cradle (Markle and Olney, 1980) in *Snyderidia*. In *Pyramodon* the anal-fin pterygiophores are elongate, more robust, and form a variable criss-crossed visceral cradle (Markle and Olney, 1980, Fig. 4), an autapomorphy (15) (Fig. 3). Carapines have much shorter dorsal- and anal-fin pterygiophores than either the outgroups or pyramodontines and they are strongly inclined anteriad (Figs. 4–6), a synapomorphy (16). A uniquely derived feature (17) of *Encheliophis* is the presence of some anterior dorsal pterygiophores that do not support fin rays (Fig. 6). Throughout the family there is a tendency for fin rays to be secondarily supported by the midpoint of the next posterior pterygiophore that may have an anteriorly directed process at the point of support (Figs. 2–6).

The dorsal-fin origin is located forward over vertebra 6 in *Brotula* (Fig. 2), 4 to 10 in the ophidiids and bythitids, and 6 to 9 in the pyramodontines and some echiodontines (Figs. 2–5, Table 4). A derived state could be attributed to taxa with dorsal-fin origins over or posterior of vertebra (VDO) 10 or ARDO > 13, conditions found in some *Echiodon* and all Carapini (Figs. 4B, 6, Table 4). However, each of these groups has a different dorsal-fin ontogeny, and thus the state for the adult dorsal-fin origin in these two groups is not homologous (see Ontogeny section).

The anal-fin origin is under vertebrae 16–21 in *Brotula*, the bythitids and the ophidiids. It is more anteriad in all carapids and under vertebrae 1–13 (Table 4), a synapomorphy (18). There seems to be a progressive trend of anterior movement of the anal-fin origin and anus, culminating in some species of Carapini (Arnold, 1956; Trott, 1970). A VAO count equal to or less than 8 is considered a derived state (19) and is found in all carapines and *P. ventralis* (Table 4).

The A_{30} and D_{30} counts (Table 4) generally track changes in dorsal- and anal-fin origins (see above). There are interesting differences in number of fin rays per

Table 4. Ranges of meristic values in juvenile and adult pearlfishes (Carapidae). Dashes indicate value is not applicable. (Abbreviations used: ND—no data)

Genus	Species	N	P ₁	A ₃₀	D ₃₀	PCV	VDO	VAO	VPB	ARDO	DRAO
<i>Pyramodon</i>	<i>ventralis</i>	12	24-26	49-53	48-51	14-15	6-7	5-8	4-6	0-5	0-4
	<i>parini</i>	14	28-30	43-47	47-51	15-16	6-7	9-11	4-7	—	7-12
	<i>punctatus</i>	11	26-28	47-51	47-51	17-19	6-7	8-10	5-7	—	3-10
	<i>lindae</i>	6	22-23	45-50	50-53	16	6-7	10-13	4-7	—	11-18
<i>Snyderidia</i>	<i>canina</i>	16	24-27	42-46	47-50	13-15	6-7	8-11	5-7	—	6-11
	<i>fowleri</i>	53	13-17	46-51	43-50	19-22	6-8	4-7	4-6	0-6	—
	<i>margaritiferae</i>	28	16-19	48-52	45-49	18-20	6-7	4-7	4-6	0-9	—
	<i>parvibrachium</i>	13	14-16	44-51	44-47	16-18	6-7	5-8	3-6	0-3	—
<i>Carapus</i>	<i>acus</i>	29	20-24	55-63	36-43	17-19	10-13	1-4	—	19-25	—
	<i>bermudensis</i>	28	17-20	53-62	36-45	17-18	10-14	2-4	—	17-25	—
	<i>mourlani</i>	40	17-21	54-61	35-41	15-17	11-14	2-4	—	18-25	—
	<i>sluiteri</i>	1	16	50	38	19	12	4	—	18	—
<i>Encheliophis</i>	<i>dubius</i>	25	16-20	47-54	35-43	19-21	11-13	3-6	—	17-22	—
	<i>homei</i>	37	17-21	53-61	33-38	16-19	12-14	1-4	—	19-26	—
	<i>boraborensis</i>	41	15-20	45-57	31-42	15-17	11-15	2-5	—	13-23	—
	<i>gracilis</i>	49	17-19	42-52	25-36	26-32	13-17	3-6	—	19-27	—
<i>Echiodon</i>	<i>sagamianus</i>	12	15-16	39-45	28-35	20-24	11-14	3-5	—	12-18	—
	<i>vermiops</i>	3	15-16	40	28	20-22	16	5	—	19-20	—
	<i>vermicularis</i>	32	—	36-43	19-27	20-23	16-19	4-6	—	17-24	—
	<i>dawsoni</i>	9	17-21	39-43	28-35	21-25	11-13	6-7	—	11-12	—
<i>Echiodon</i>	<i>exsilium</i>	7	20-21	47-50	38-42	21-25	10-11	6-7	—	8-10	—
	unnamed species*	6	20-21	45-47	32-33	ND	14-15	6-8	—	16-19	—
	<i>coheni</i>	3	15-18	52-54	42-45	18-19	9-10	4	—	10-13	—
	<i>pukaki</i>	1	25-26	49	36-38	26	11	6	ND	11	—
<i>Echiodon</i>	<i>pegasus</i>	4	14-16	41-46	37-38	28-29	11-12	7-9	—	6	—
	<i>cryomargarites</i>	11	19-21	46-50	35-40	25-29	11-12	6-8	—	9-12	—
	<i>dentatus</i>	9	15-17	47-50	42-45	26-28	8-9	5-7	7-8	3-6	—
	<i>drummondi</i>	21	15-17	46-51	42-47	26-29	8-9	6-8	7-8	2-7	—
<i>Eurypleuron</i>	<i>neotes</i>	1	19-20	47	38	35	8	8	ND	—	—
	<i>rendahli</i>	8	14-17	37-38	40-43	31-35	7-8	5-8	6-7	0-4	—
	<i>owasianum</i>	15	15-20	37-44	36-47	22-27	7-8	5-7	6-7	0-6	—

* Data taken from larval material since adults are unknown.

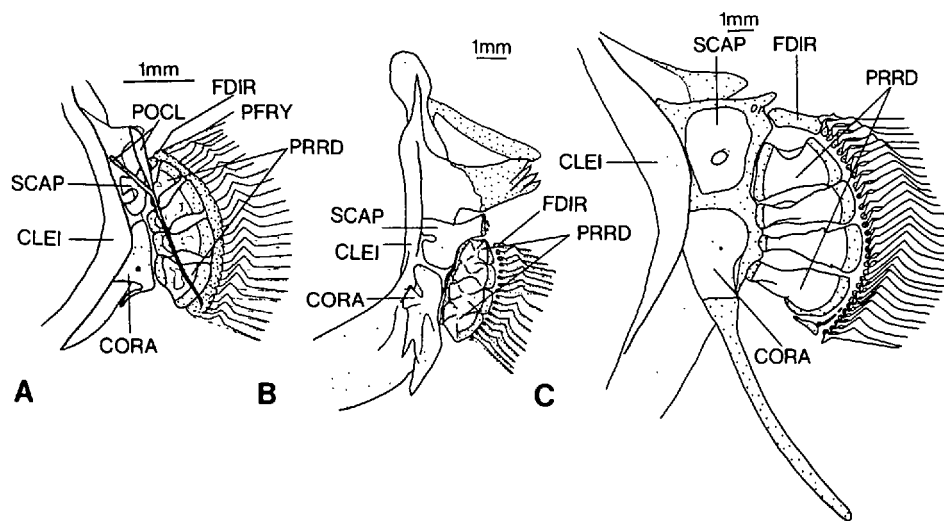


Figure 9. Pectoral fin skeleton in A) *Brotula multibarbata* AMS uncat., 53.8 mm SL; B) *Ophidium omostigmum* UF 34270; C) *Pyramodon parini* USNM 298306.

vertebra which can be useful for some taxonomic studies of carapids. For example, pyramodontines average 2.1–2.5 anal-fin rays per vertebra while carapines average 1.6–2.1. Reduction in number of vertical-fin elements per vertebra appears to have taken place several times in carapines. The closely related (though not sister) taxa, *Echiodon dawsoni* and *Ec. exsilium*, have very similar fin origins but significantly different, non-overlapping ranges of A_{30} (Table 4) due to a much lower ratio of fin elements to vertebra in *Ec. dawsoni* (1.7–1.8) as compared to *Ec. exsilium* (2.0–2.1). Other taxa with one or both ratios low (<1.9) are *Eurypleuron*, *Echiodon rendahli*, *Ec. neotes* and *Encheliophis*.

Counts of DRAO and ARDO also tend to track vertical-fin origins with modification because of differences in vertical-fin element to vertebra ratios (Table 4). All ophidiiforms (Cohen and Nielsen, 1978), including some carapids (Table 4), have the dorsal-fin origin in advance of the anal-fin origin and, therefore, cannot have ARDO counts. For those carapid taxa with ARDO values, interspecific variation in this character can be largely due to variation in abdominal shape or, in some Carapini, to variation in the number of dorsal pterygiophores lacking fin rays (Fig. 6). Despite this variability, there is a strong tendency for increasing values in the carapines culminating in ARDO counts >13 (20) in the Carapini (and see the above discussion of homology in dorsal-fin origins). High DRAO values are found in *P. lindas* (Fig. 2) as well as in the outgroups.

Pectoral-fin Girdle (Figs. 9–12).—*Brotula* and *Dicrolene* have two postcleithra and in *Brotulataenia* there is a single postcleithrum (Cohen, 1974). Carapids and other ophidiids lack postcleithra (Figs. 9–12). An elongate ventral process of the coracoid appears to be a functional analogue of postcleithra in carapids (Figs. 9–12). An identical relationship of presence of the ventral process of the coracoid and absence of postcleithra is seen in salmoniforms (Markle, unpubl. obs.). Thus, in carapids, the coracoid process appears to be a larval structure retained since postcleithra do not develop. It attains its greatest development in larval *Eurypleuron*, where it supports the larval exterilium gut (see Larval Morphology section, below). The process, in a reduced state, is also present in *Brotula* where it is aligned with the

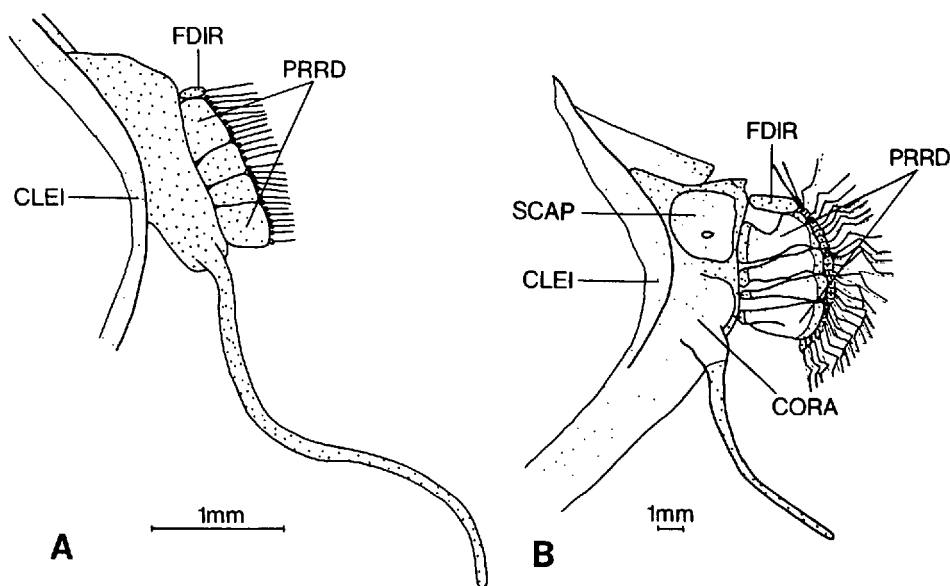


Figure 10. Development of the pectoral fin skeleton in *Snyderidia canina* A) USNM 219344 5.7 mm HL, B) USNM 214033 33.9 mm HL.

cleithrum (Fig. 9). Although the process is longer, a similar alignment is found in some Echiodontini (Fig. 11B, C). The process angles away from the cleithrum in all other carapids (Figs. 9–12).

The scapula of *Brotula* is Y-shaped with a foramen partly bounded by the cleithrum and a distal articular surface supporting the first fin ray and its distal radial (Fig. 9A). The ophiidiid and bythiid scapulae are similar to that of *Brotula* but may not support a fin ray (Fig. 9B). In carapids, the scapula is not autogenous but is part of the coraco-scapular cartilage and is bounded on its dorsal surface by cartilage (Figs. 9, 10, 12), a synapomorphy (21). The scapula contains a foramen except in *Onuxodon* where the loss of the scapular foramen (Fig. 11C) is derived (22). Since the scapula develops within the coraco-scapular cartilage, a cartilaginous dorsal boundary on the scapula ontogenetically would precede an ossified one (Fig. 10). Thus, the absence of cartilage dorsal to the scapula is considered a synapomorphy (23) in *Eurypleuron*, *Echiodon* and *Onuxodon* (Fig. 11). At the upper posterior corner of the coraco-scapular cartilage is generally a medially-directed process. It is variously developed in carapids (Figs. 9–12) but is uniquely boot-shaped in *Onuxodon* (Fig. 11C), a synapomorphy (24).

In the pectoral fin of *Brotula*, the bythiids and ophiidiids (Fig. 9A, B), there are four proximal radials, each moderately constricted (but secondarily fused in ophiidiids), and a distal radial supporting each fin ray. The upper proximal radial is the smallest radial in *Brotula* and the ophiidiids whereas in carapids it varies from subequal to the largest (Figs. 9–12). The greatly enlarged first proximal radial of the Carapini is unusual among most teleost lines (Starks, 1930) and is a synapomorphy (25). A sub-rectangular first proximal radial is found in *Brotula* and the pyramodontines (Figs. 9, 10). In the carapines it is D-shaped with a cartilaginous, arched dorsal surface (Figs. 11, 12), a synapomorphy (26). In echiodontines, the ventral surface of the lower proximal radial is cartilaginous (Fig. 11), a synapomorphy (27).

In all carapids the first (most dorsal) distal radial is greatly enlarged (Figs. 9–

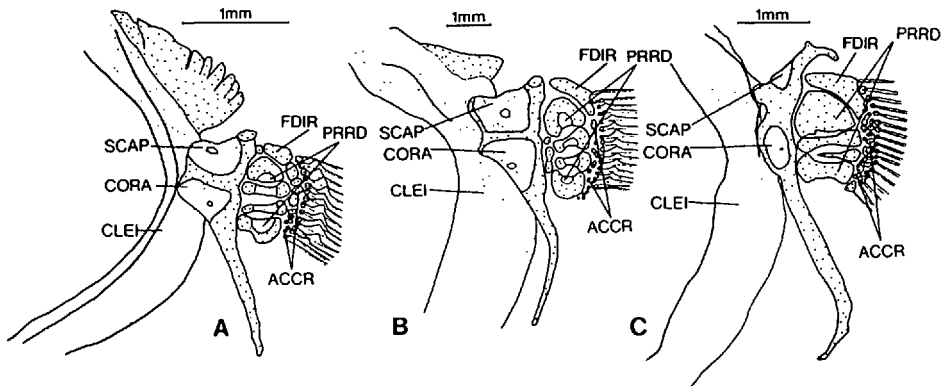


Figure 11. Pectoral fin skeleton in A) *Echiodon dawsoni* UF 30886, B) *Ec. drummondi* DAFS uncat., C) *Onuxodon fowleri* OS 11059.

12), a synapomorphy (28). The first distal radial otherwise retains the same relationship to the upper fin ray and scapula as in *Brotula*. This distal radial is so large that in some carapines it supports two or more rays (the second and subsequent rays with associated distal radials) (Figs. 11–12). There are numerous distal radials in echiodontines (Fig. 11), a synapomorphy (29). *Pyramodon parini* may also develop a few extra distal radials ventrally (Fig. 9C), but these are not as extensive as in the echiodontines, and we do not equate the two conditions.

Pectoral-fin ray counts are in the mid-20s in *Brotula* (Fig. 9A), *Brotulataenia* (Cohen, 1974), some ophidiids (Gordon et al., 1984), pyramodontines and two carapine species (*Carapus acus* and *Echiodon pukaki*, Table 3). We assign three derived states to pectoral-fin ray counts: >28, an autapomorphy of *Pyramodon parini* (30); equal to 0, an autapomorphy of *Encheliophis vermicularis* (31); and equal to or less than 21, a derived state in all carapines except *C. acus* and *Ec. pukaki* (32).

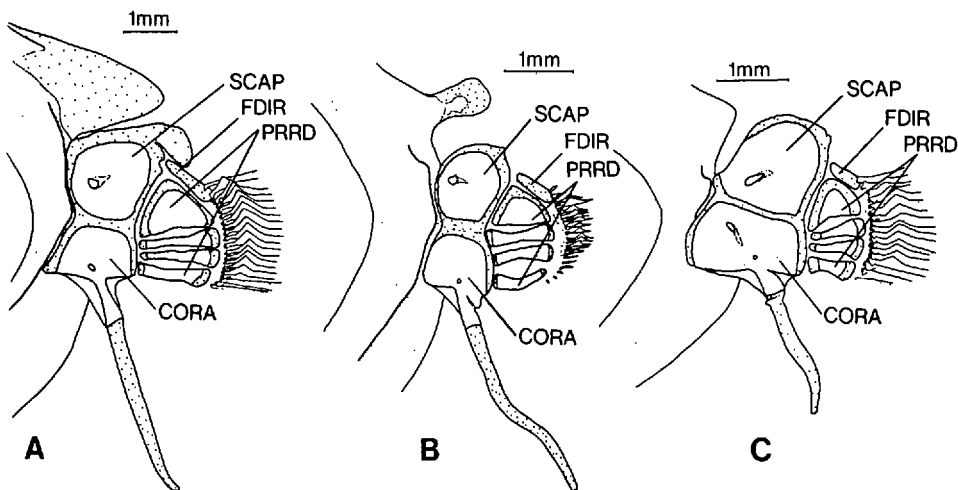


Figure 12. Pectoral fin skeleton in A) *Carapus moulani* ZMUC CN20, B) *Encheliophis boraborensis* CAS 48978, C) *En. gracilis* UF 34265.

Table 5. Ranges of meristic values in larval pearlfishes. Dashes indicate value is not applicable. Abbreviation used: ND—no data or not developed in size range observed. Values of HL expressed in mm. With the single exception noted in the footnote, all data are based on cleared and stained specimens

Genus	Species	N	P ₁	A ₅₀	D ₅₀	PCV	VVO	VDO	VAO	ARDO	DRAO	HL range
<i>Pyramodon</i>	spp.	2	27-29	50	50	17	6	7	8	—	—	4.4-6.0
<i>Snyderidia</i>	<i>canina</i>	2	25	46	51	ND	6	7	9	—	6-9	3.6-5.7
<i>Onuxodon</i>	<i>fowleri</i>	6	17	52-55	45-46	19-24	5-8	7-8	6	6-8	—	2.9-5.4
	<i>parvibrachium</i>	4	16-18	51-53	46-49	18-20	4-6	7	7-8	0-3	2-4	4.4-5.4
<i>Carapus</i>	<i>acus</i>	1	ND	ND	ND	ND	4	11	3	18	—	3.1
	<i>bermudensis</i>	3	19	53-58	39-42	17-18	4-5	10-11	6-7	13-18	—	4.6-4.9
<i>Encheliophis</i>	<i>dubius</i>	1	20	52	37	19	4	12	6	18	—	3.5
<i>Echiodon</i>	<i>dawsoni</i>	2	18	38	29-30	ND	11	11-12	6	10-11	—	3.7-3.9
	<i>exsilium</i>	2	21-25	50-51	39-42	ND	9-10	10-11	6-7	9-11	—	4.8-5.9
	unnamed	6	20-21	45-47	32-33	ND	14	14-15	6-8	16-19	—	3.3-4.3
	<i>coheni</i>	7	ND	52-55	40-42	19-20	9-10	10	5	12-14	—	2.2-3.2
	<i>cryomargarites</i>	2	ND	45	39-40	26-28	10	11	8	6-7	—	4.4-4.5
	<i>dentatus</i>	5	ND	48-50	44-45	ND	7-8	8-9	7-8	5	—	4.3-5.7
	<i>drummondi</i>	1	ND	48	43	ND	8	9	8	4	—	4.6
	<i>rendahlit*</i>	4	14-15	45	40-41	30-35	7	8	6-8	5-6	—	5.7
<i>Eurypleuron</i>	<i>owasianum</i>	2	ND	42	44-45	ND	7	8	8	2	—	3.5-5.5

* Except P₁ and PCV, all counts based on myomere examination.

Short pectoral fins are characteristic of ophidiiforms (Cohen and Nielsen, 1978). Long pectoral fins are derived and found in *Pyramodon parini*, *P. ventralis*, *S. canina* and *Echiodon cryomargarites* (33) (see species accounts below).

In *Echiodon exsilium* pectoral-fin rays appear to be lost ontogenetically (Tables 4, 5, see species account below). Since developmental series were available for only some species, this character cannot be verified in all carapid taxa. Nevertheless, we treat this as an autapomorphy of *Ec. exsilium* (34).

Pelvic Fins.—Pelvic fins are present in most ophidiiforms (Cohen and Nielsen, 1978) and *Pyramodon*. We interpret the loss of pelvic fins to be derived (35) and independently lost in *Snyderidia* and carapines. The equally parsimonious alternative that a loss of pelvic fins is a carapid synapomorphy coupled with an atavistic reversal in *Pyramodon* violates Dollo's Law (Mayr, 1969), the principle that evolution is irreversible to the extent that structures once lost are difficult to regain. Dollo's Law has some validity in cases involving reappearance of complex homologous structures, especially when the original loss was from larval as well as adult stages (Hennig, 1966). Williams (1984b) noted that adult echiodontines lack pelvic bones. This loss, a synapomorphy of echiodontines (36), occurs ontogenetically, presumably by resorption, since the pelvic cartilage is present in all carapid larvae examined.

Hyoid Arch (Fig. 13).—The hyoid arch in *Brotula* consists of a slim, rod-like interhyal, triangular epihyal, sub-rectangular ceratohyal, two hypohyals that meet a strut from the ceratohyal, and eight branchiostegal rays, four articulating laterally and four articulating medially (Fig. 13A). The ventral hypohyal forms a cup-like recess which receives the cartilaginous, anterior extension of the ceratohyal (Fig. 13A).

The ophidiids and carapids have seven branchiostegal rays, four articulating laterally on the epihyal and posterior ceratohyal and three articulating medially on the shaft of the ceratohyal (Fig. 13B–E).

The epihyal-ceratohyal joint is sutured in the ophidiids, pyramodontines (Fig. 13B) and *Encheliophis boraborensis*. Suturing occurs late in ontogeny and we interpret lack of suturing as a carapine synapomorphy (37). Sutures were secondarily acquired in *En. boraborensis* which, like pyramodontines, attains a relatively large size. This character may represent a type of heterochrony in which a late forming character does not receive expression in those taxa that have a small adult body size.

Both hypohyals participate in the ceratohyal strut joint in ophidiids and most carapids. In ophidiids there is a tendency for more of the dorsal hypohyal to participate while in *Onuxodon* and some *Echiodon* (Fig. 13D, E) there is a greater participation by the ventral hypohyal. Both hypohyals retain contact with the ceratohyal strut in *Ec. dentatus*, *Ec. dawsoni*, and *Eurypleuron* (Fig. 13C).

In the outgroups as well as most carapids the branchiostegal membranes are separate. In five species of *Encheliophis* (*boraborensis*, *sagamianus*, *vermiops*, *vermicularis*, and *gracilis*) the branchiostegal membranes are partly or wholly united, a synapomorphy (38) (see species accounts).

Gill Arches (Figs. 14–20).—Ventral gill arches of carapids do not seem to deviate from the arrangement in other ophidiiforms (Figs. 14, 15). Variation within carapids is in presence or absence of dentition on the third basibranchial and presence or absence of long gill rakers (sensu Cohen and Nielsen, 1978) on the first arch. There are no teeth on the third basibranchial in *Echiodon*, *Onuxodon* or some *Encheliophis* (*boraborensis*, *sagamianus*, *vermiops*, *vermicularis*, and *gracilis*) (39).

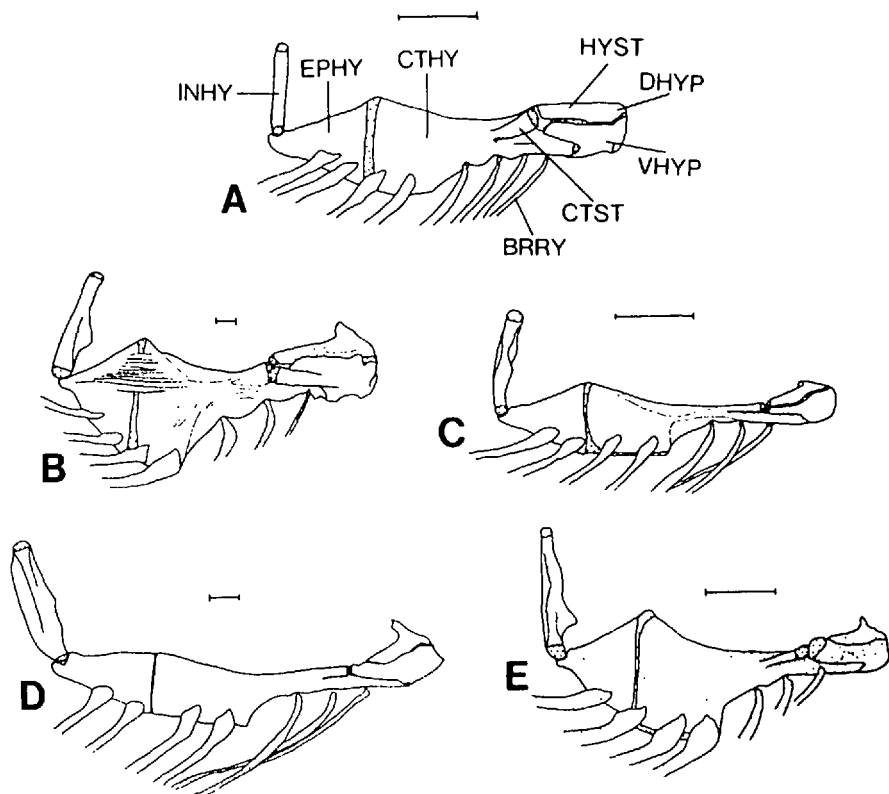


Figure 13. Hyoid arch in A) *Brotula multibarbata* AMS uncat., 53.8 mm SL; B) *Snyderidia canina* USNM 214033, C) *Echiodon dawsoni* UF 30886, D) *Ec. drummondi* DAFS uncat., E) *Onuxodon fowleri* OS 11059.

All carapids have three developed gill rakers on the first arch, except the following species of *Encheliophis* which have none (*sagamianus*, *vermiops*, *vermicularis*, and *gracilis*) (40). Teeth are always present on the fifth ceratobranchial. A plate-like urohyal is suspended medially between the ceratohyals of each side; its anterior extent at about the tips of the ceratohyal strut (Fig. 15).

The dorsal gill arch of *Brotula* (Fig. 16A–C) has three basically rod-like pharyngobranchials and a tooth patch of a fourth. It is similar to *Brotulataenia* as described by Cohen (1974: fig. 5). During development, the third pharyngobranchial broadens and its toothplate fuses with the second pharyngobranchial (Fig. 16B–C). Teeth are present on all but the first pharyngobranchial. The first epi-branchial has a well-developed uncinat process in contact with the second pharyngobranchial.

In ophiidiids, bythitids and carapids, an interarcual element develops between the uncinat process of the first epi-branchial and the second pharyngobranchial (Travers, 1981). It is cartilaginous in ophiidiids and pyramodontines (Fig. 17), and ossified in carapines (Figs. 19–20), the latter a synapomorphy (41). In *Snyderidia* the interarcual element fits inside a cup-like receptacle formed on the uncinat process of the first epi-branchial (Fig. 18), an autapomorphy (42).

The interarcual element is much smaller than the first epi-branchial in ophiidiids and pyramodontines, about 60% of the first epi-branchial in echiodontines (Figs.

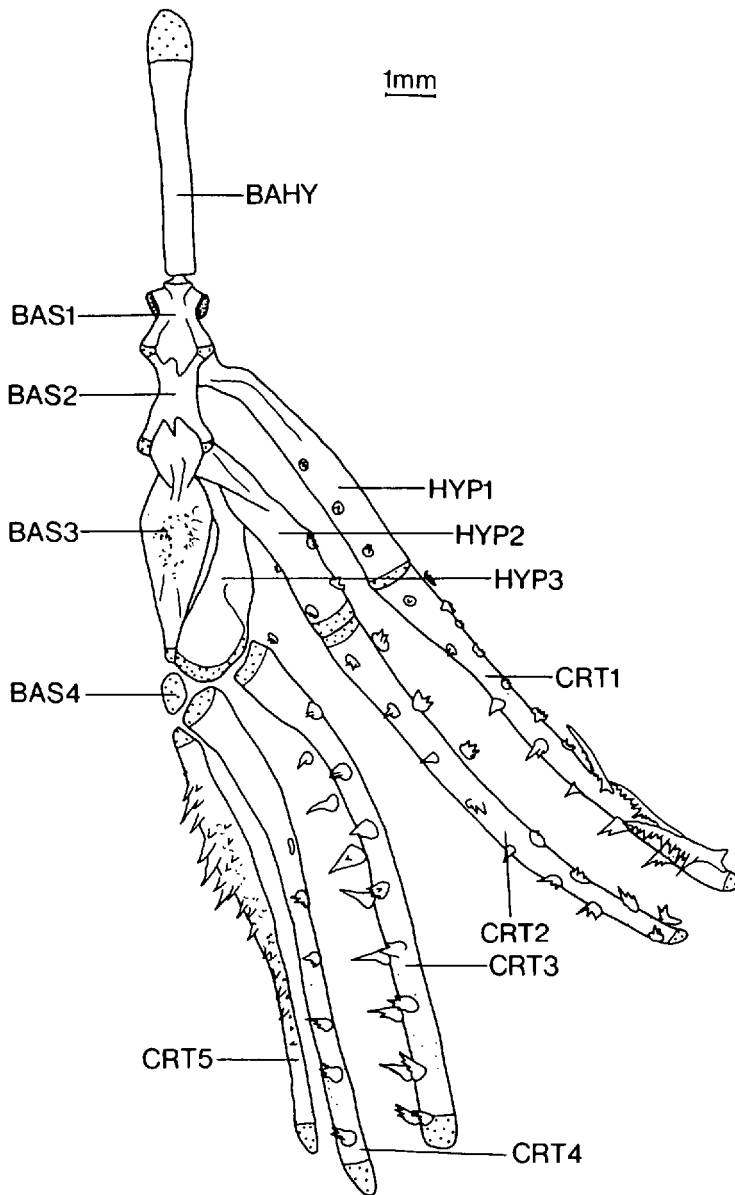


Figure 14. Ventral gill arch of *Snyderidia canina* USNM 214033.

19, 20B), and about equal to or longer than the first epibranchial in the Carapini (Fig. 20A). A similar, structurally related, trend is found in the site of articulation between the interarcual element and first epibranchial. It is located midway or further up the epibranchial in ophidiids, very high (near the distal end) in pyramodontines (Fig. 17), low in the echiodontines (Figs. 19, 20B) and very low in the Carapini (Fig. 20A). We define derived character states of this complex as follows: an interarcual element about 60% of the length of the first epibranchial and articulating relatively low on the first epibranchial is a synapomorphy of echio-

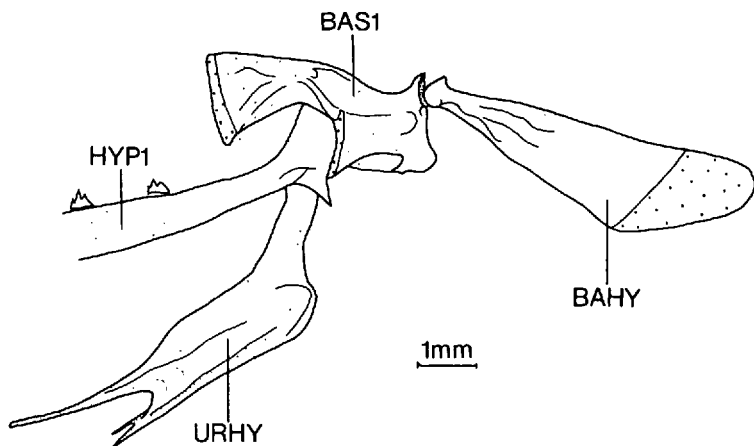


Figure 15. Left lateral view of the anterior basibranchials in *Synderidia canina* USNM 214033.

odontines (43); while an interarcual element equal to or longer than the first epibranchial and articulating very low on the first epibranchial is a synapomorphy of the Carapini (44).

The interarcual element seems to develop as a chondrification and/or ossification of an interarcual ligament (Markle, 1989). The ligament normally joins the uncinate process of the first epibranchial to the second pharyngobranchial. In carapids we found two additional ligaments associated with the interarcual element. In pyramodontines, a ligament attaches proximally to the interarcual cartilage and connects it with the second epibranchial (Fig. 17). In *Onuxodon*, a similar (but difficult to see) ligament runs from the interarcual element to a process on the first epibranchial (Fig. 19). We could not consistently find these ligaments. Both arrangements seem unique. Additional cross-connecting ligaments between epibranchials are seen in most carapids and seem worthy of more detailed study.

The second epibranchial has a flange in all forms except *Onuxodon* (Fig. 19B) where we consider the loss an autapomorphy (45).

Orbit and Ethmoid Region (Figs. 21–23).—The relationships of bones in this region are complex. Several derived character states are evident and these will be discussed with reference to *Brotula*, the ophidiids and development as seen in *Onuxodon*.

In *Brotula*, the ophidiids and early in carapid ontogeny, the cranium between

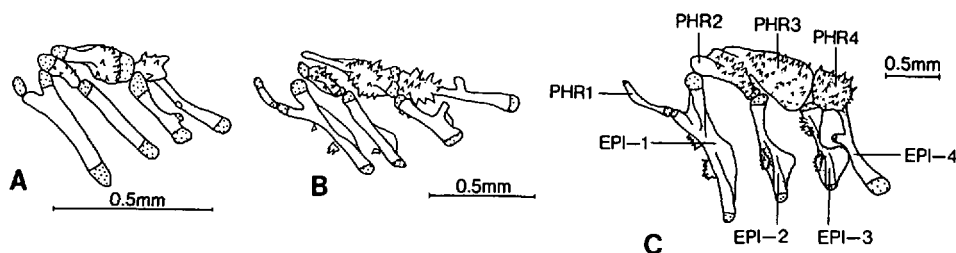


Figure 16. Development of the dorsal gill arch of *Brotula multibarbata* AMS uncat. A) 12.6 mm NL, B) 21.0 mm SL, C) 53.8 mm SL.

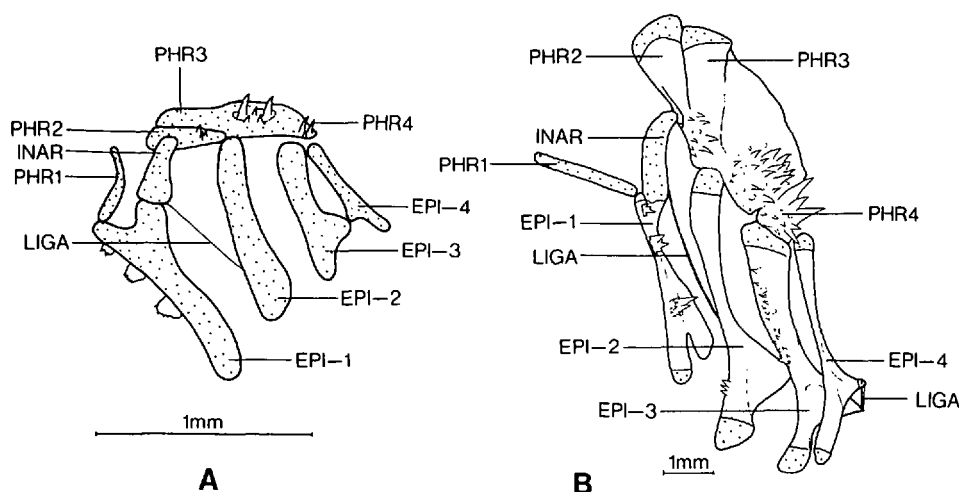


Figure 17. Development of the dorsal gill arch in *Snyderidia canina* A) USNM 219344, 5.9 mm HL, B) USNM 214033, 33.9 mm HL.

the orbits is completely open (cross-hatched areas in Fig. 21A, B). In the largest *Brotula* (53.8 mm) and the ophidiids this opening does not close over with bone, although strong connective tissue does close the opening in some of the ophidiids. In most carapids the opening is at least partly closed by ventro-medial growth of both frontals which come together above the intraorbital space (Fig. 21B, C). The interorbital section of the frontal is the site of origin for the large extrinsic swim-bladder muscle (Courtenay and McKittrick, 1970). In *Snyderidia*, and some *Echiodon* the interorbital section of the frontals forms a somewhat plate-like flange partly occluding the interorbital space (Figs. 22A, B, 23A). *Echiodon dawsoni* is the only exception since the adults show no closure of the frontals (Fig. 22C). Other small species of *Echiodon* such as *Ec. neotes*, and *Ec.* unnamed may also exhibit this character, but the absence of material precludes any conclusive statement. The state in *Ec. dawsoni* appears to be heterochronic.

The lateral ethmoid of *Brotula* develops as a saddle-shaped structure (Fig. 21A) and becomes plate-like as the concave area fills in with bone. A plate-like lateral ethmoid is found in adults of ophidiids and all carapids except the Carapini where it is U-shaped (Fig. 23B, C). The U-shaped condition is considered derived (46).

The ethmoid develops a pronounced bump in *Brotula* and echiodontines (Figs. 21, 22) while pyramodontines and Carapini have a rounded ethmoid (Fig. 23). We consider this condition (47) to be homoplastic, acknowledging the equally parsimonious alternative of atavistic reversal in the echiodontines.

The basisphenoid normally has a foramen. It is lost ontogenetically in *Onuxodon* (Fig. 21B, C) and is considered a synapomorphy (48).

Cheek and Jaws (Figs. 24–28).—The premaxilla is toothed, excludes the maxilla from the gape, and primitively has a flange which provides medial support to the maxilla which is subequal in size (Fig. 24). In the Carapini the maxilla is reduced in size to a slim rod-like bone, whereas the premaxilla is much wider, the flange much expanded and providing medial support over a greater length of the maxilla (Fig. 26B) (49). An adnate maxilla is found in four species of *Encheliophis* (*sagamianus*, *vermiops*, *vermicularis*, and *gracilis*), a synapomorphy (50). A supra-maxilla is present in *Brotula*, *Brotulataenia* and other ophidiids and its absence

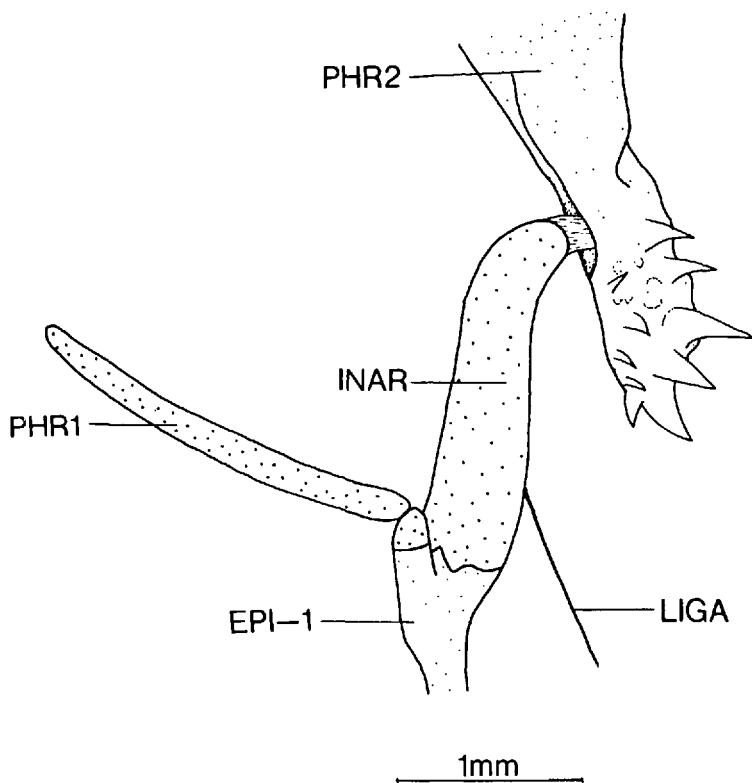


Figure 18. Detail of the interarcual element in *Snyderidia canina* USNM 214033.

in carapids is considered a synapomorphy (51). A premaxillary (rostral) cartilage is found in all ophidiiforms. Late in ontogeny, the cartilage becomes partly ossified in *Pyramodon* and *Snyderidia* (Fig. 25A, B), a synapomorphy (52).

Premaxillary teeth are small and conical in *Brotula* (Fig. 24) and the ophidiids. Fang-like teeth develop at the symphysis of both jaws in pyramodontines and echiodontines (Figs. 25B, 26A, 30), a derived state (53) that may have evolved independently in pyramodontines and echiodontines. We acknowledge the equally parsimonious alternative that these fang-like teeth may be a family synapomorphy

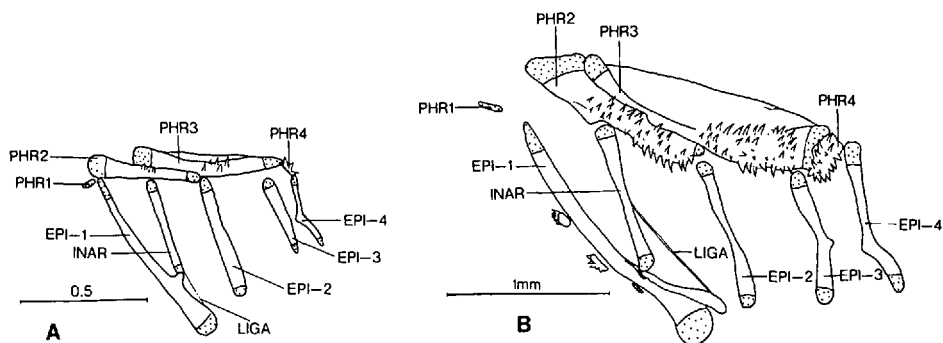


Figure 19. Development of the dorsal gill arch in *Onuxodon fowleri* A) 11.4 mm HL, VIMS 8274, 3.6 mm HL, B) OS 11059.

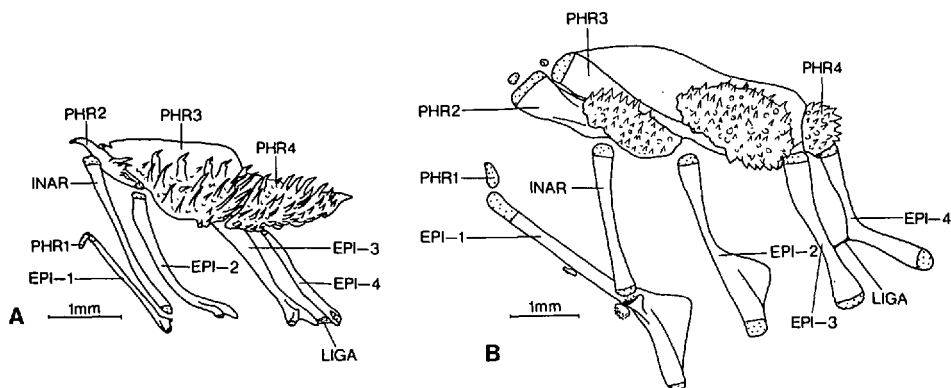


Figure 20. Dorsal gill arch in A) *Encheliophis gracilis* UF 34265, B) *Echiodon drummondi* DAFS uncat.

that was secondarily lost in the Carapini. Highly specialized “cardiform” teeth are found in the Carapini (Figs. 26B, 27) (54). Cardiform teeth are restricted to the symphysis in *Carapus* but are all along the premaxilla in *Encheliophis*.

A coronomeckelian bone is found in *Brotula*, *Brotulataenia* and most carapines. It rests on Meckle’s cartilage in *Carapus* and *Encheliophis* (Fig. 26B) and is free in *Echiodon* and *Onuxodon* (Fig. 26A). It is independently lost in the pyramodontines and *Eurypleuron* (55).

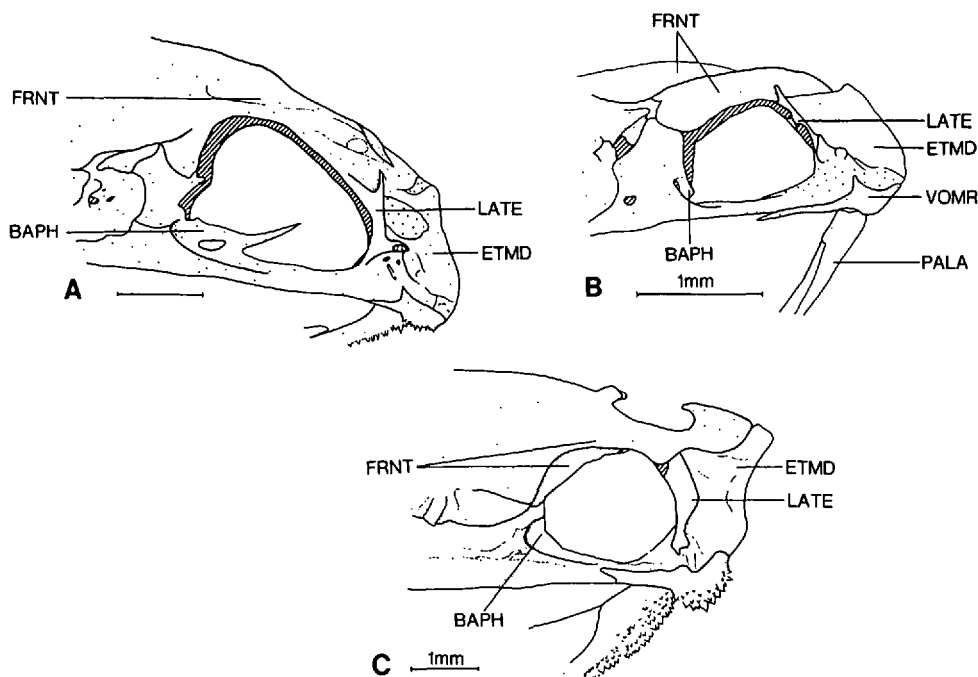


Figure 21. Right lateral view (somewhat rotated around long axis) of the orbit and ethmoid region in A) *Brotula multibarбата* AMS uncat., 53.8 mm SL, B) *Onuxodon parvibrachium* VIMS 8275, C) *O. fowleri* OS 11059. Cross-hatched area indicates the open cranial area between the orbits.

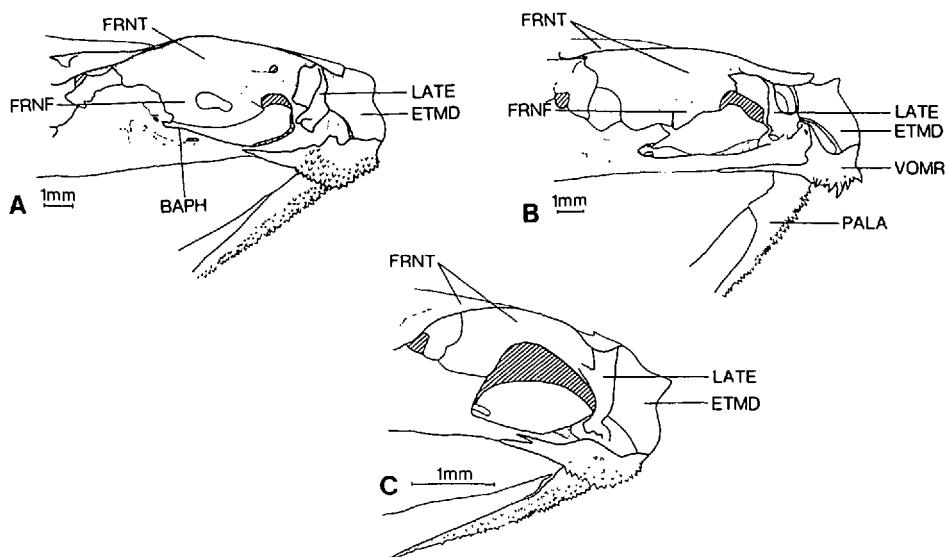


Figure 22. Right lateral view (somewhat rotated around long axis) of the orbit and ethmoid region in A) *Eurypleuron owasianum* AMS 16574-003, B) *Echiodon cryomargarites* ISH 1818/68, C) *Ec. dawsoni* GMBL 78-102. Cross-hatched area indicates the open cranial area between the orbits.

All ophidiiforms have a ligamentous interhyal-interopercle connection (Fig. 28). A process on the interopercle receives the ligament. The process is least, if at all, developed in species of *Encheliophis* (Fig. 26B).

All ophidiiforms have a V-shaped opercle (Figs. 24–26). Near its articulation with the hyomandibular, there is sometimes a small opercular foramen in pyramo-

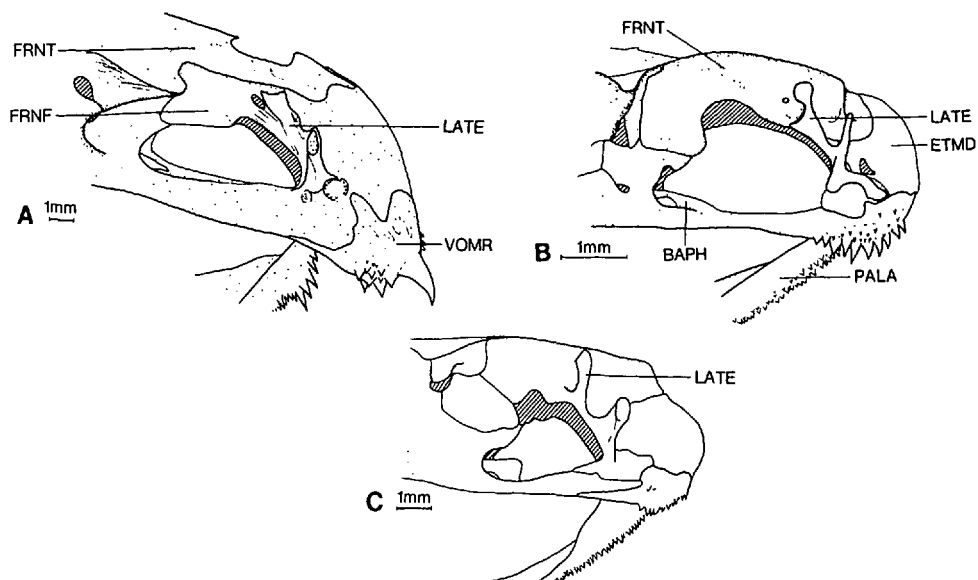


Figure 23. Right lateral view (somewhat rotated) of the orbit and ethmoid region in A) *Snyderidia canina* USNM 214033, B) *Carapus bermudensis* AMNH 7627, C) *Encheliophis sagamianus* MCZ 30750.

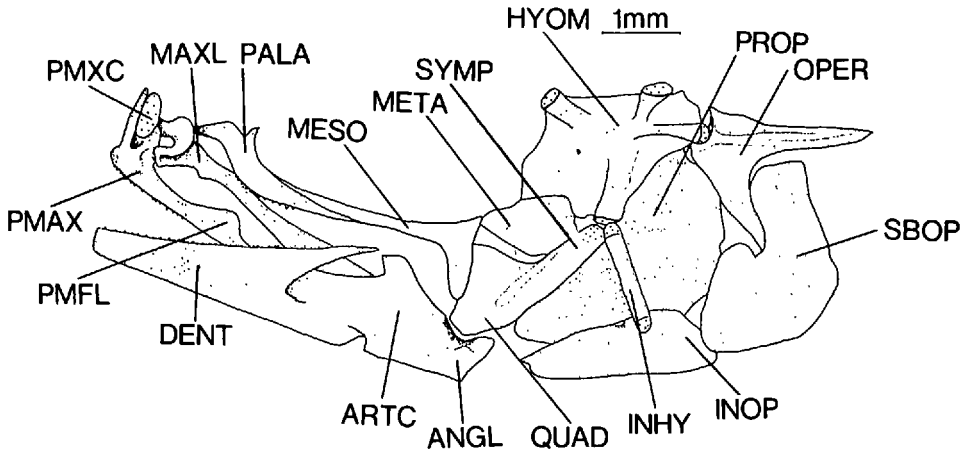


Figure 24. Cheek and jaws of *Brotula multibarbata* AMS uncat., 53.8 mm SL.

dontines and carapines (Figs. 25, 26B). The pointed upper part of the opercle has been reported to project through an elliptical slit in some species of *Echiodon* by Williams (1984).

In *Brotula* there is a small foramen in the anterior field of the hyomandibular (Fig. 24). In ophidiids it is also small and located close to the anterior edge of the bone. A large hyomandibular foramen (Figs. 25, 26) is a carapid synapomorphy (56). The foramen passes partly through the anterior hyomandibular shaft in pyramodontines and echiodontines (Figs. 25B, 26A) and below the shaft in Carapini (Fig. 26B).

Swimbladder

Length (Figs. 2–6, 29–35).—Swimbladder length is highly variable in ophidiiforms. In general it seems to correlate with precaudal vertebral number and perhaps that is the only way to ascribe polarity to its various states. In *Brotula* (Fig. 2A) and *Pyramodon* (Fig. 3A) it is of moderate size (to the 12th or 13th centrum) and both of these taxa have presumably primitive precaudal vertebral counts (see above). *Snyderidia* has a greatly reduced swimbladder length (Fig. 2B) which we interpret as derived (57) since its sister group (*Pyramodon*), subfamily sister group (carapines) and the family outgroups all have moderate to long swimbladders.

Carapines have generally long swimbladders taking up the greater portion (usually more than 90%) of the visceral cavity (Figs. 4–6, 31–35), a synapomorphy (58). The condition is reversed in *Encheliophis sagamianus* and *En. vermiops*. These carapines have a swimbladder that is reduced in size and bulbous (Fig. 34A, B). In *En. sagamianus* it reaches only to the 12th centrum and occupies about 55% of the gut cavity. *Onuxodon* is unique in having its bulbous posterior section (Fig. 5) embedded in hypaxial muscles rather than suspended in the visceral cavity, a synapomorphy (59).

Constrictions.—Two types of constrictions occur in carapid swimbladders: a “bottleneck” type which delimits a small anterior section from a relatively large posterior section; and an “intrinsic” type which appears as a narrow, elastic-looking band that delimits two subequal sections of swimbladder or a large anterior section from a smaller posterior section.

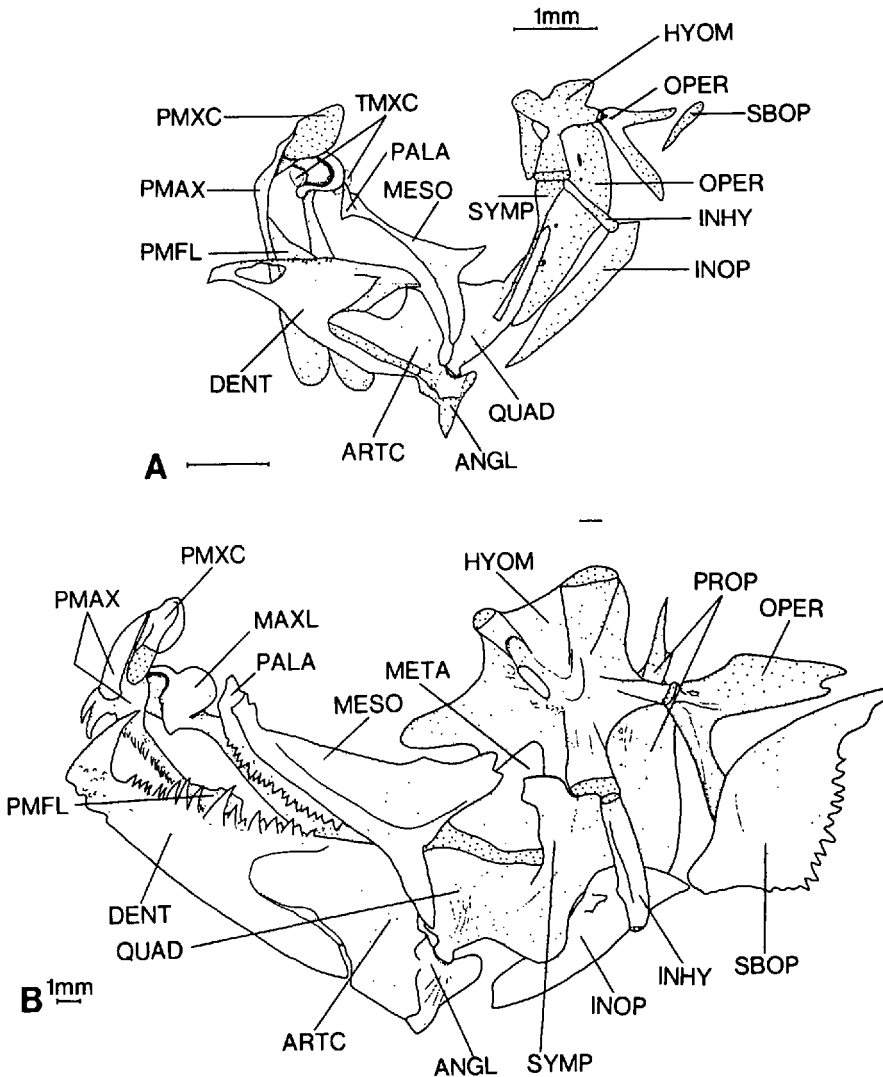


Figure 25. Check and jaws of *Snyderidia canina* A) USNM 219344, 5.7 mm HL, B) USNM 214033, 31.5 mm HL.

Brotula has a "bottleneck" constriction (Fig. 29A) as do the ophidiids and some carapids. In the outgroups the constriction is around the fifth or sixth centrum. In a number of ophidiiforms, a swimbladder-derived ossification, the rocker bone has evolved. In ophidiids that have a rocker bone, the structure is, like the "bottleneck" constriction, found under the fifth or sixth centrum (Rose, 1961). In carapids, a "bottleneck" constricted swimbladder is found in *Snyderidia* and echiodontines (Markle et al., 1983) positioned under the third centrum (Fig. 29B). In *Onuxodon*, the rocker bone is also located under the third centrum (Figs. 5, 30). Markle et al. (1983) suggested that the sclerified structures of the anterior swimbladder of *Echiodon cryomargarites* were precursors to the rocker bone of *Onuxodon*. Svetovidov (1961) also suggested that the rocker bone, as well as the anterior swimbladder "plate" of *Ophidion*, was a swimbladder "ossification."

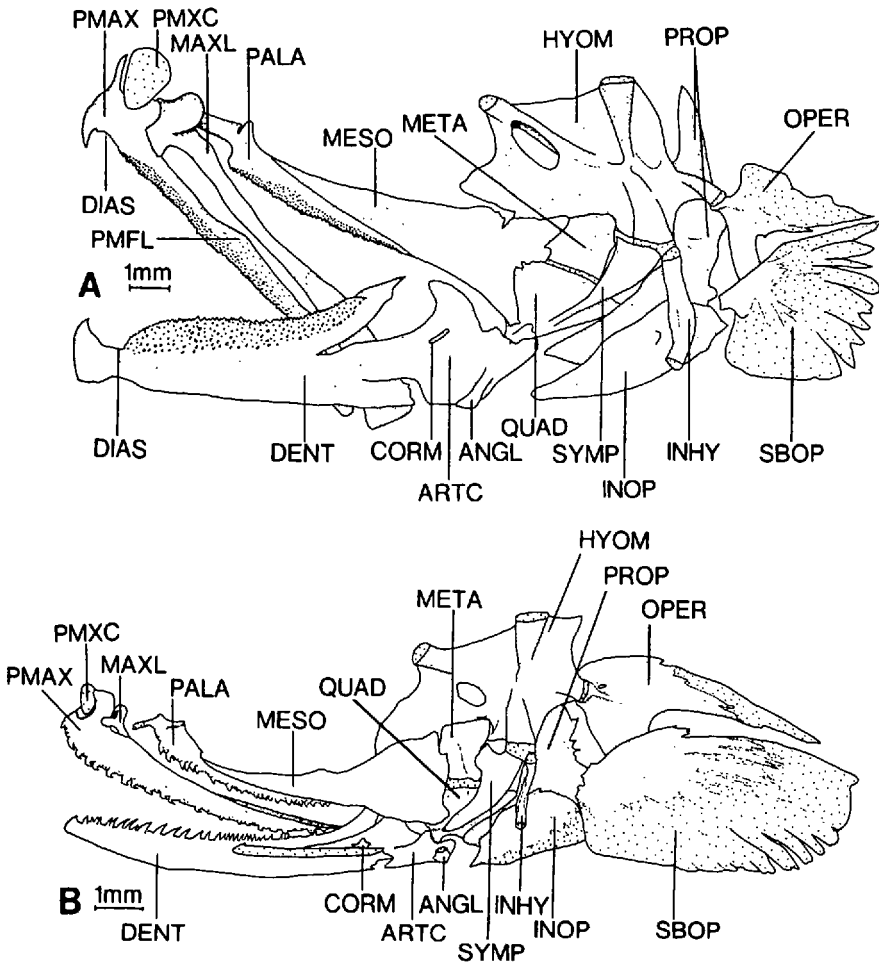


Figure 26. Cheek and jaws of A) *Echiodon dentatus* MMF 22377, B) *Encheliophis gracilis* UF 34265.

Despite its complexity, apparent origin from the swimbladder, and even the identical ligament arrangement between the first two ribs in *Onuxodon* (Fig. 5) and *Ophidion* (Rose, 1961: fig. 6), we are not prepared to interpret the rocker bone as a synapomorphy of *Onuxodon* and *Ophidion*. The only evidence in support of our interpretation of parallel development, aside from the differences which separate the two families, is the difference in rocker bone position relative to vertebral centra. Therefore, at the level of Carapidae, we interpret sclerification of the anterior swimbladder as synapomorphic for echiodontines (60) and the rocker bone as synapomorphic for *Onuxodon* (61). Both characters are homoplastic at the level of Ophidiiformes and seem to indicate a latent capacity to develop these structures within different ophidiiform lineages. Our interpretation is in contrast to that of Courtenay and McKittrick (1970), who believed that similarity in patterns of specializations, notably the rocker bones of *Onuxodon* and *Ophidion*, indicated a common ancestor for carapids and sound-producing ophidiids. Those authors could have been suggesting that the rocker bone was an ophidiiform synapomorphy, independently lost in all but two genera, or that

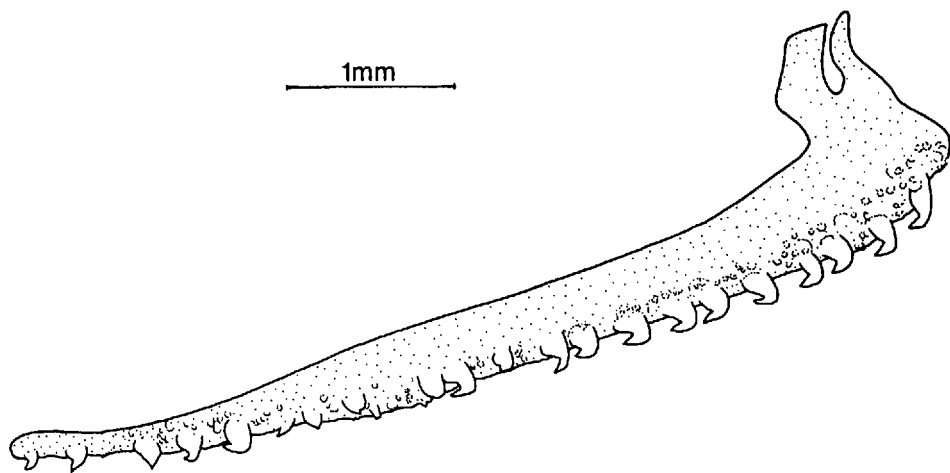


Figure 27. Premaxilla with cardiform teeth in *Encheliophis gracilis* UF 34265.

ophidiiforms have the propensity to develop rocker bones under some conditions. We believe the latter is true but acknowledge that "propensities" are not rigorous characters.

An "intrinsic" constriction is only found in some species of *Echiodon* and *Carapus* (Figs. 31, 32A, 35). In *Echiodon drummondi*, *Ec. dentatus* and *Ec. rendahli* the constriction is posteriad and delimits a small posterior chamber, a synapomorphy (62). In addition, the character is sexually dimorphic, appearing only in males of *Ec. drummondi* and *Ec. dentatus*. In *Carapus* the constriction is central, delimits two subequal chambers, is found in both sexes and we interpret it as a different derived character (63). In both groups the constriction appears restricted to the swimbladder wall (tunic) and does not cut off the swimbladder lumen.

Other Characters.—A swimbladder specialization of *Encheliophis* is the presence of a thin, membranous, posterior terminal bulb (Figs. 32B, 33, 34), a synapomorphy (64). It may be a gas resorption area or play some role in sound production, but we have not investigated its microstructure or function.

In *Echiodon*, parallel tunic ridges (synapomorphy 65) are located on the ventral midline or left lateral surface of the posterior part of the swimbladder (Fig. 35). These are thickened portions of tunic bounded on either side by thinned, narrow regions of tunic, and we are unable to ascribe function to these structures. We did not observe tunic ridges in any vexillifers or tenuis larvae of *Echiodon* and have no information on the size at first appearance of this character.

Ontogeny

Growth Stages.—The named life history stages of carapids (vexillifer, tenuis and adult) are eco-morphological. Arnold (1956) defined the stages using a plot of total length against head length of *C. acus* for material found in various habitats (Fig. 36). Trott (1981) subsequently defined the tenuis stage as follows: "The vexillifer elongates into the tenuis stage, which concurrently becomes demersal. . . . The tenuis larva shortens, then elongates again and becomes somewhat thicker-bodied through the juvenile to the adult stage."

We believe some revision and refinement of terminology is necessary for the

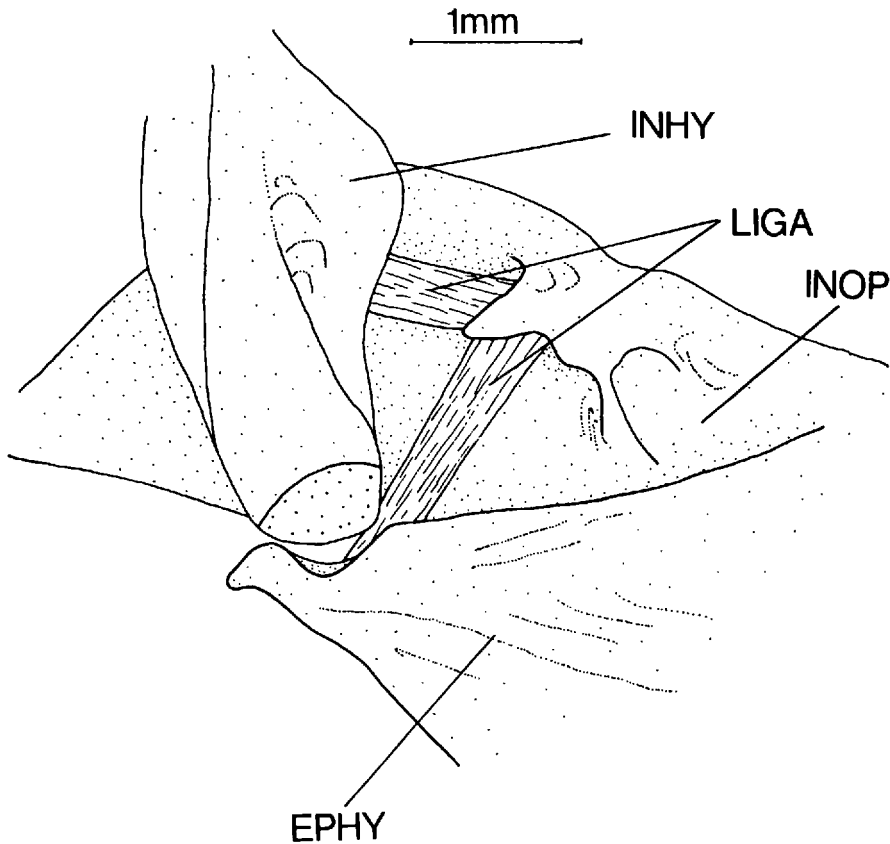


Figure 28. Detail of the interhyal-interopercle connection in *Synderidia canina* USNM 214033.

sake of clarity. Unlike Arnold (1956) we have not found tenuis stages longer than the longest larval stage (see *Carapus bermudensis* section, Fig. 93 below). In fact, the longest larvae found in many *Carapus* correspond very well in size with the maximum elongation phase of Arnold's "tenuis," about 180–200 mm (Fig. 36). Also, we do not find universal occurrence of the tenuis stage in carapids. It does not occur in pyramodontines and appears to be greatly abbreviated in *Eurypleuron*, some *Echiodon*, and *Onuxodon* (see genus and species accounts). We would define the tenuis stage as a demersal or transitory pelagic-demersal stage during which total length is reduced. The presence of a tenuis stage is a synapomorphy of carapines (66). We interpret the spectacular reduction in length in the Carapini (larval length is reduced by about 50%) as an additional derived state (67).

Vexillifers are a planktonic larval stage possessing a highly modified, deciduous first dorsal ray or vexillum (Govoni et al., 1984). The larval form is unique to carapids (Markle and Olney, 1980; Gordon et al., 1984), but the phylogenetic information is found in the vexillum (see below) rather than the larval form. Vexillifers may have distinct growth stages as described above or there may be no change in growth characteristics when the vexillum is lost or resorbed, as in *Pyramodon*. In vexillifers of *Carapus*, growth becomes exponential, "overshooting" the adult "growth program" (see genus and species accounts). It is the exponential larval growth uncoupled from adult growth constraints that "requires"

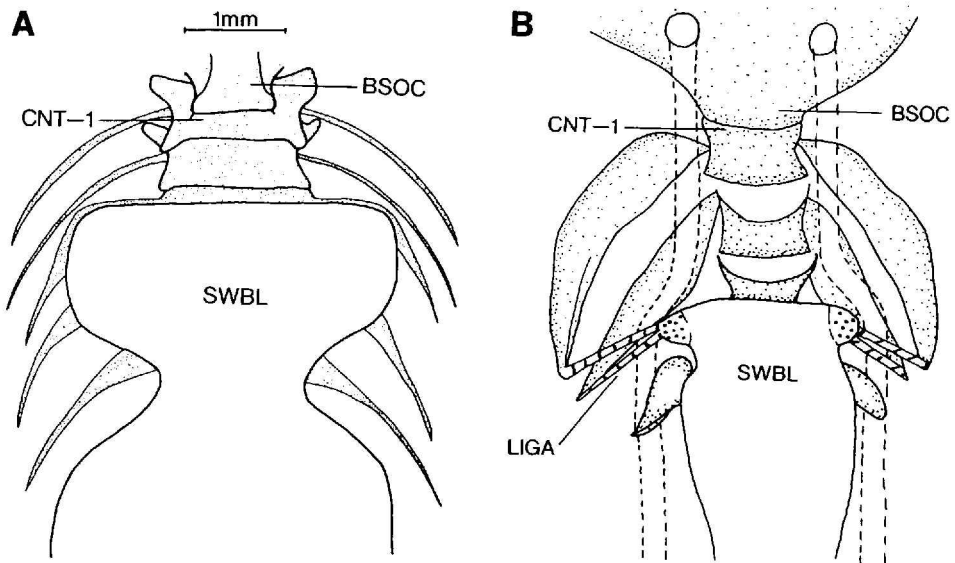


Figure 29. Ventral view of the anterior swimbladder in A) *Brotula barbata* UF 34271, B) *Echiodon cryomargarites* LACM 20984-3.

a compensatory, “shrinking” tenuis stage in some carapids. Further work, including weight and vertebral number changes (if any) during the tenuis transition, would help to clarify the metamorphic process in carapids.

Growth rate in vexillifers, estimated using unverified “daily” increments in

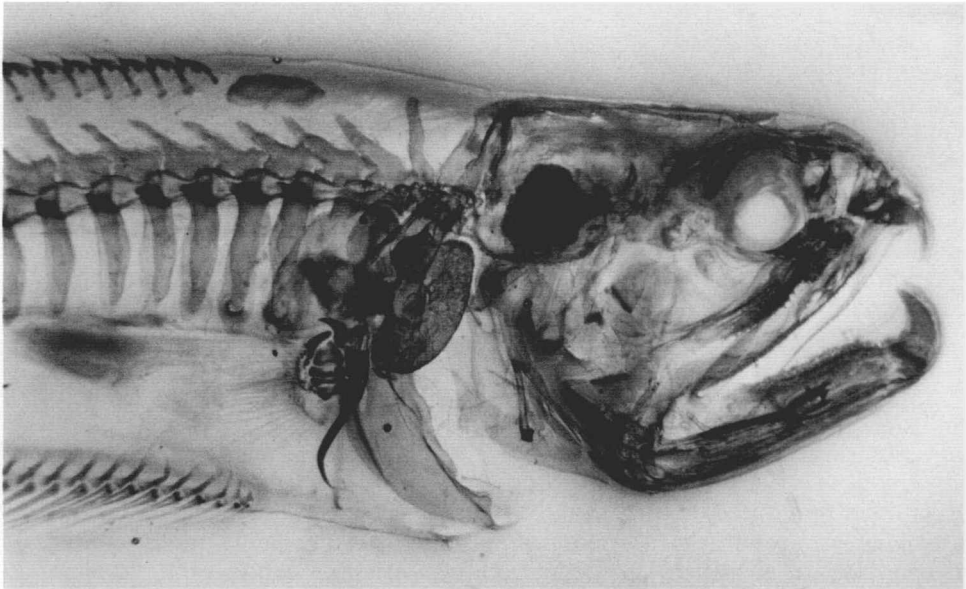


Figure 30. Anterior skeleton of *Onuxodon fowleri* CAS 48976.

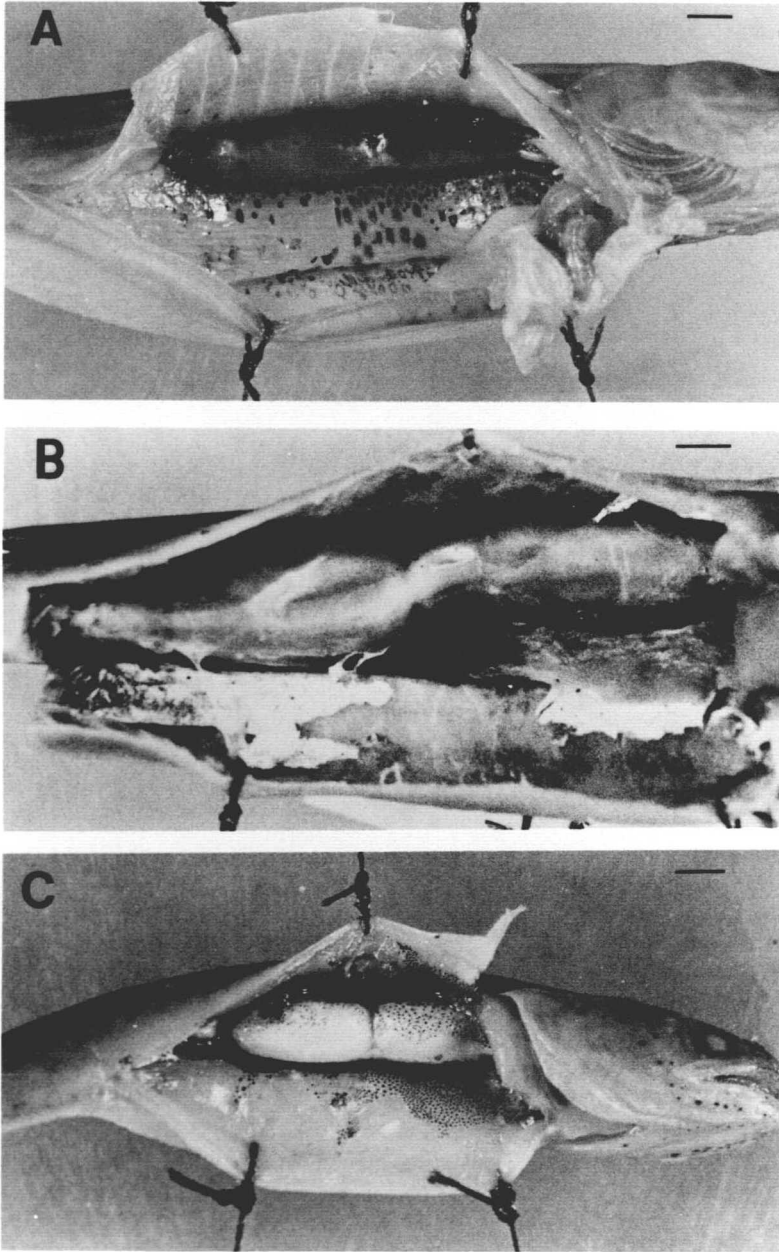


Figure 31. The swimbladder of A) *Carapus bermudensis* AMNH 37388, B) *C. acus* ZMUC CN34-37, C) *C. mourlani* ZMUC CN 15-19. Scales equal 2 mm.

otoliths of *Echiodon dawsoni*, suggests that a head length of 4.3 mm is reached in about 100 days (J. Govoni, pers. comm. 30 March 1984).

Maximum adult size tends to decrease from almost 60 mm HL in pyramodontines to about 30 mm HL in carapines. The smallest adults are in *Onuxodon*, some species of *Echiodon* (less than 15 mm HL) and *Encheliophis vermiops* (less

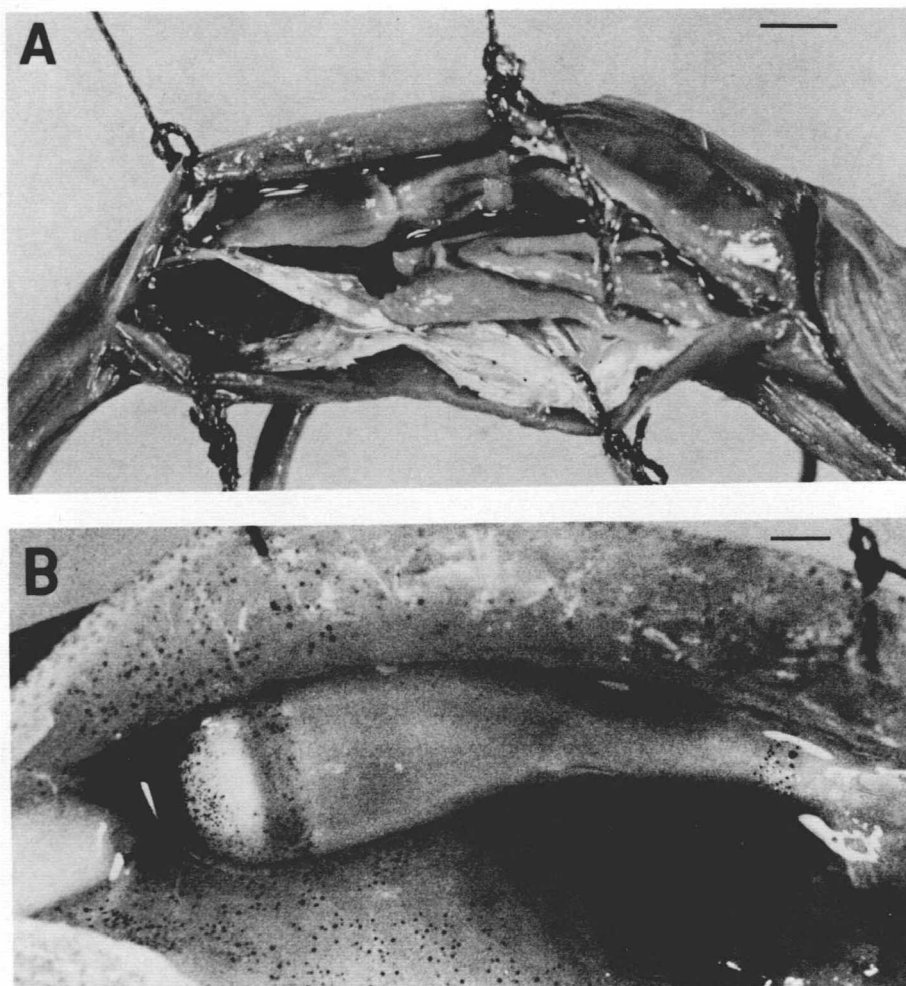


Figure 32. The swimbladder of A) *Carapus sluiteri* ZMA 112.679, B) *Encheliophis boraborensis* VIMS 8281. Scales equal 2 mm.

than 10 mm HL). This essentially neotenic-like trend apparently shows maximum expression in the small species of *Echiodon*, where the interorbital space does not close (Fig. 22C, above) and where one species may retain the vexillum (see *Ec. neotes* section).

Adult shapes are moderately variable but always tapering posteriad (see species accounts below). In cross section through the trunk, most species are moderately compressed. *Onuxodon* is very compressed and *Encheliophis* may be robust (*En. boraborensis*) to round (*En. vermiops*).

Egg and Larval Morphology.—EGGS. Carapid eggs, like ophidiiform eggs in general, have not been well described. Gordon et al. (1984) summarized the sparse literature. Few generalizations about carapid eggs are well founded, but future workers should be aware of at least five characters: 1) eggs may be released in a mucilaginous raft; 2) yolk is described or illustrated as segmented; 3) an oil globule is present; 4) egg shape is oval or ellipsoid; and 5) the embryo is frequently

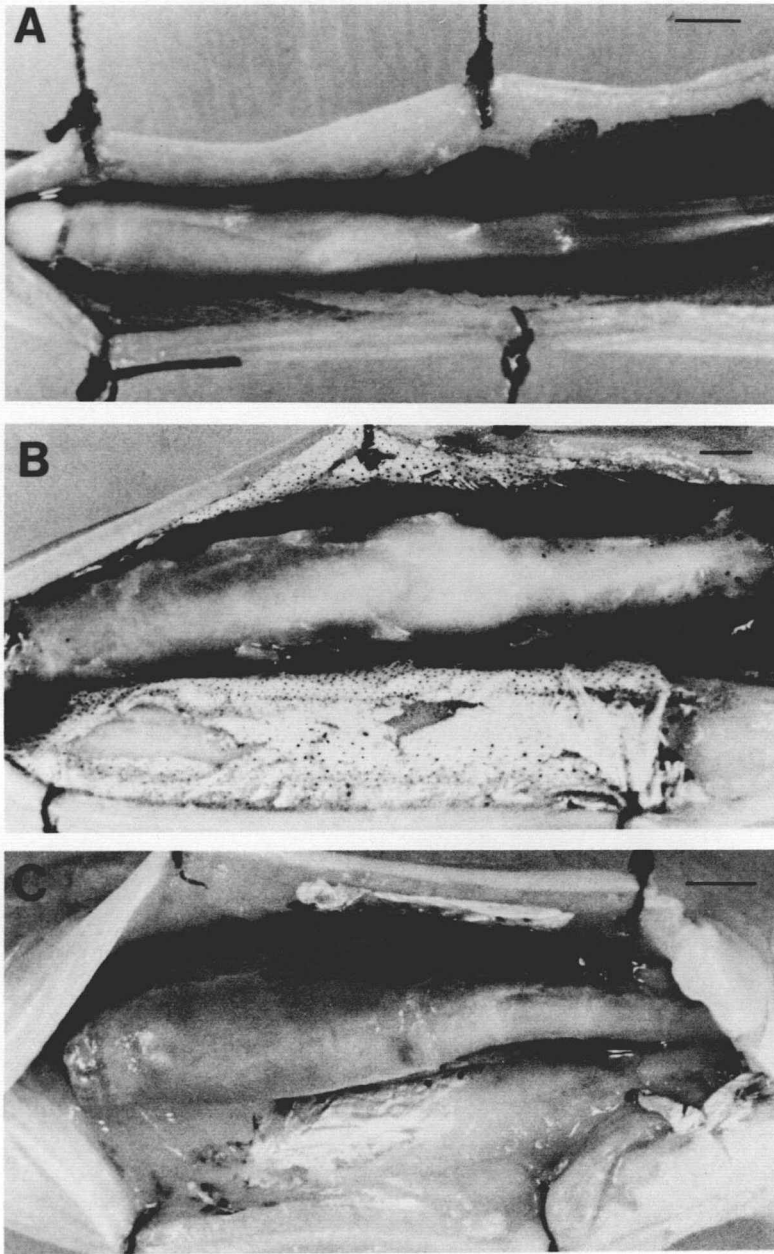


Figure 33. The swimbladder of A) *Encheliophis gracilis* VIMS 8280, B) *En. homei* NMV A843, C) *En. dubius* CAS 48984 Scales equal 2 mm.

pigmented. There appears to be much to learn about carapid egg morphology. Robertson (1975) and Brownell (1979) apparently both described eggs of *Eurypleuron owasianum*, but their observations on the presence or absence of oil globules and a mucilaginous raft differed.

VEXILLUM. The presence of a vexillum in the larval stage is a synapomorphy

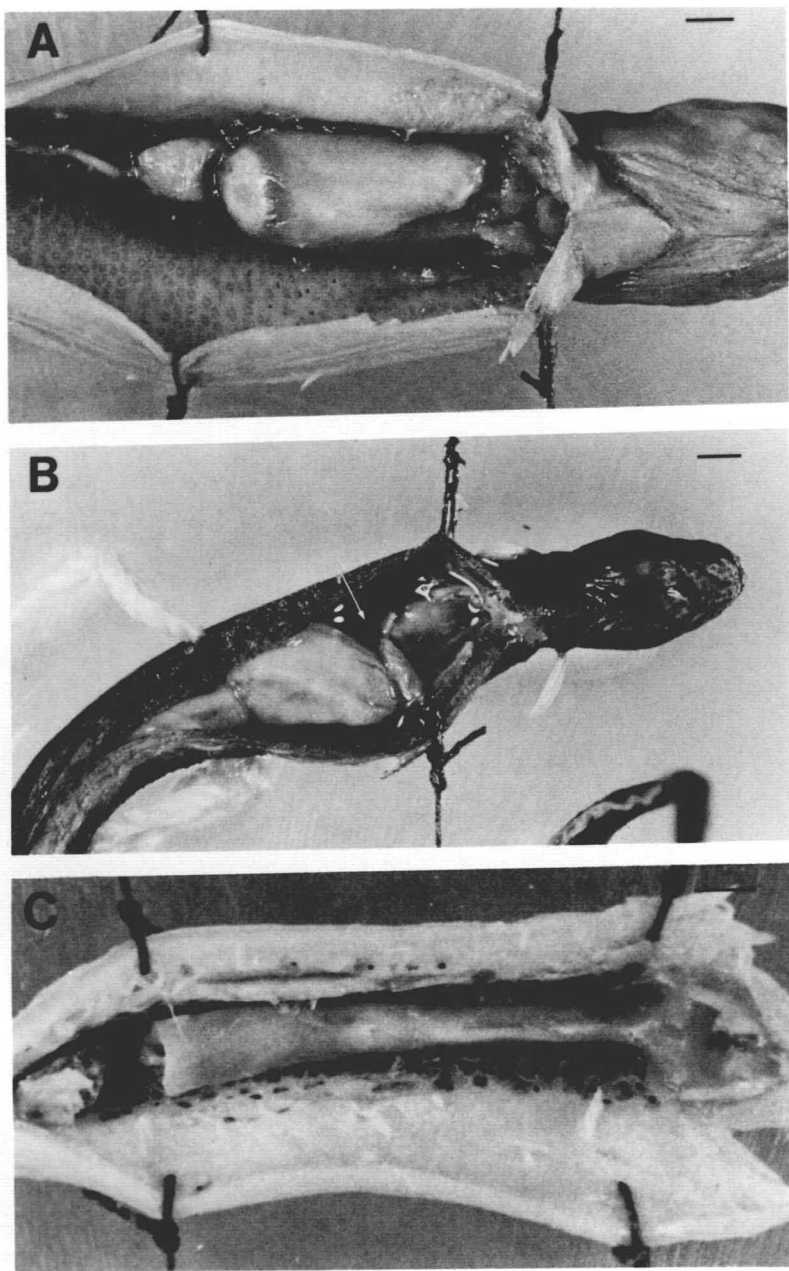


Figure 34. The swimbladder of A) *Encheliophis sagamianus* MCZ 30750, B) *En. vermiops* AMS 5244, C) *En. vermicularis* VIMS 8282.

of the Carapidae (68). The structure of the vexillum was described in detail by Govoni et al. (1984) and characterized as a "complex larval specialization of the dorsal fin" that is singular, elongate, motile, well vascularized, innervated by a cranial nerve with no apparent spinal innervation, and resorbed or deciduously lost, or both, at metamorphosis. Observations by Curtsinger in Govoni et al.

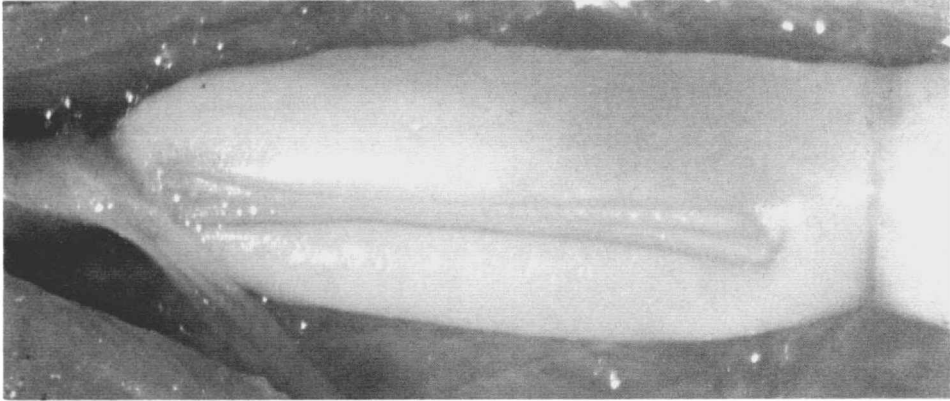


Figure 35. Tunic ridges and intrinsic constriction on the posterior swimbladder of a male specimen of *Echiodon dentatus* MMF 22434.

(1984) indicate that it is an erectile structure and the larva is able to control its length.

We originally described the vexillum as having proximal and distal segments (Olney and Markle, 1979), but subsequently have discovered completely unsegmented vexilla in a few specimens. We are unsure of the significance of these observations.

The vexillum may be highly ornamented, but its distal section is extremely fragile (Govoni et al., 1984), and it is unlikely that species specific differences in vexillar ornamentation (if such traits exist), will ever be clearly understood. In situ observations on a single specimen of *Eurypleuron owasianum* by R. Kuiter (pers. comm.) and several specimens of *Carapus* and/or *Onuxodon* (see below and Fig. 37) by Curtsinger in Govoni et al. (1984) show similarities and differences. Both observers indicate vexilla were elaborately ornamented with fleshy protuberances and pigment (Fig. 37). Kuiter's larva, in addition, had large pigment blotches laterally and was observed in a siphonophore aggregation. Siphonophore mimicry has been suggested as one function of elongate larval appendages (Kendall et al., 1984) but such speculations are largely untested. Curtsinger's larvae were not in a siphonophore assemblage, and his repeated observations over a number of days did not reveal any association of larvae with other zooplankton species.

During ontogeny the vexillum, or at least its anlage, is present shortly after hatching in *Eu. owasianum* (Robertson, 1975; Brownell, 1979) and *Ec. drummondii* (Kennedy and Champ, 1971). It is probably present early in the development of all species. The fate of the vexillum at metamorphosis is less clear, and Govoni et al. (1984) were unable to resolve the question. Resorption of the larval vexillar radial in the Carapini argues for resorption of the appendage, whereas the absence of sequential reduction of vexillar length in larger larvae argues for deciduous loss of the structure (Govoni et al., 1984). Possibly some parts are lost deciduously while others are resorbed.

The vexillar radial itself is a complex structure. In some taxa (pyramodontines and some echiodontines), it is simple and provides direct support only to the vexillum and secondary (indirect) support to one or more subsequent radials and fin rays (Markle and Olney, 1980; Gordon et al., 1984; Fig. 38). In five species of *Echiodon* for which larvae are known (see genus account and Figs. 38, 39), a compound (i.e., fused) vexillar radial provides direct support to the vexillum and

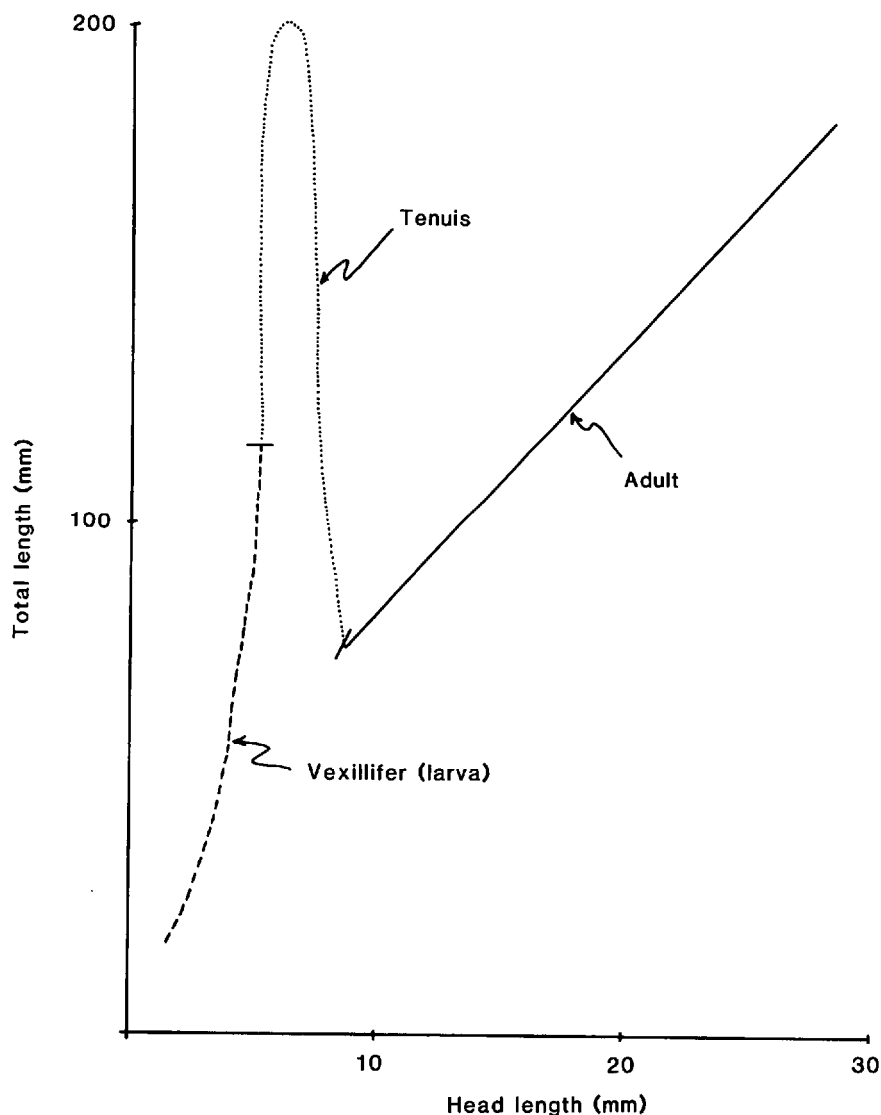


Figure 36. Diagrammatic representation of vexillifer, tenuis and adult growth patterns as proposed by Arnold (1956).

one or more subsequent fin rays. In these species a "predorsal bone," which, in carapids, is the adult remnant of the vexillar radial, does not exist because it is part of the first "adult" dorsal fin radial (see Osteology section).

We interpret the various conditions of the vexillar radial or predorsal bone as follows. First, outgroup comparison is problematical since a questionably homologous structure is found in *Brotulataenia*. All known carapid larvae have a radial supporting the vexillum and, since remnants of the radial are observed in adults in both subfamilies, we consider the ontogenetic loss of the radial as a synapomorphy of *Carapus* and *Encheliophis* (69). We also consider the more complex condition of a compound radial supporting both the vexillum and the first adult dorsal fin ray as a synapomorphy of all *Echiodon* except *drummondi* and *dentatus* (70).

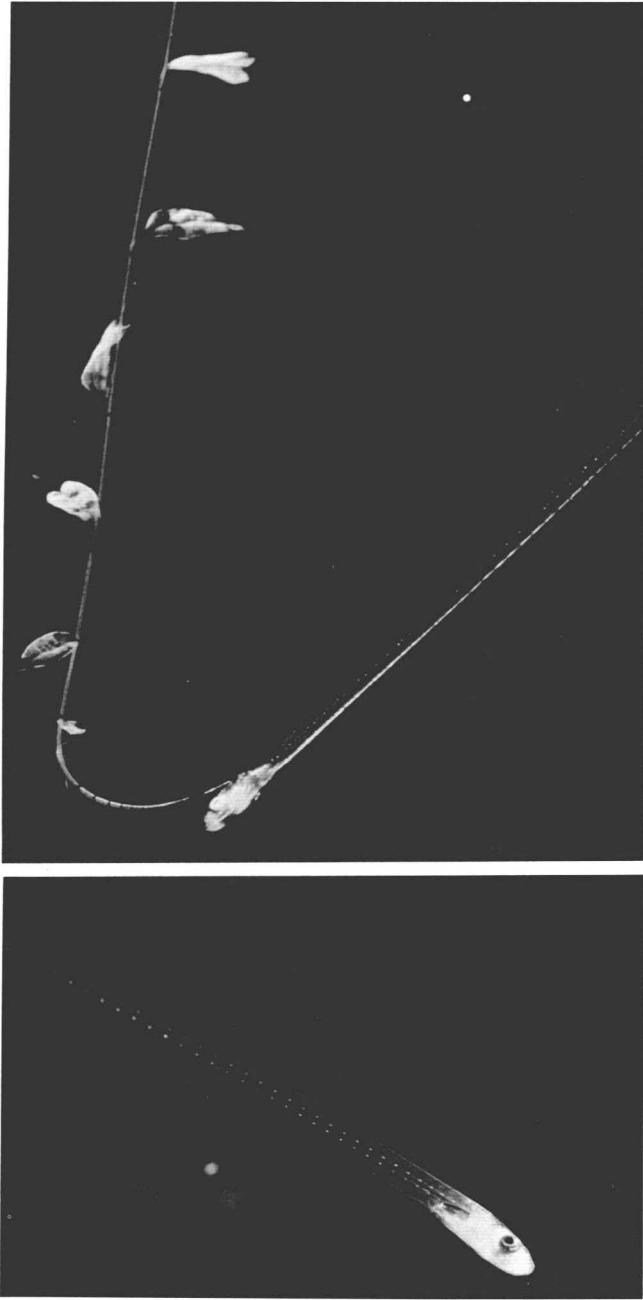


Figure 37. In situ photographs of Hawaiian pearlfish larvae. Upper: unidentified vexillifer, Lower: unidentified tenuis larva.

The position of the vexillum relative to vertebrae (myomeres), the anal fin origin, and the first normal dorsal-fin ray is useful for species identification and phylogenetic analysis. In the pyramodontines and some echiodontines, the vexillum and dorsal-fin origin are over or in advance of the anal-fin origin and all

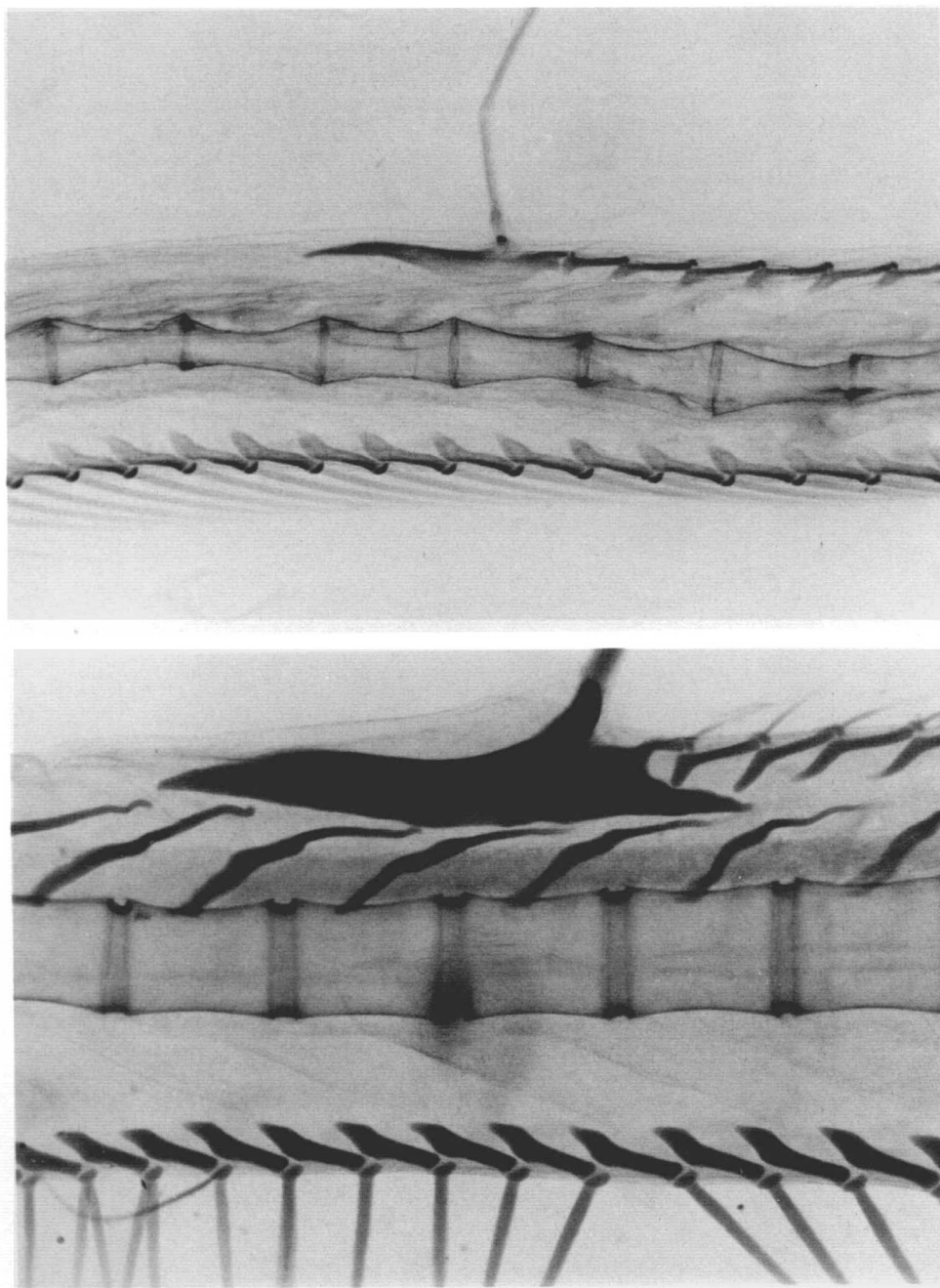


Figure 38. Photomicrograph of the axial skeleton and vexillar support in Upper: *Echiodon* unnamed ORIT uncat., 3.7 mm HL. Lower: *Ec. coheni*, VIMS 8278, 3.2 mm HL.

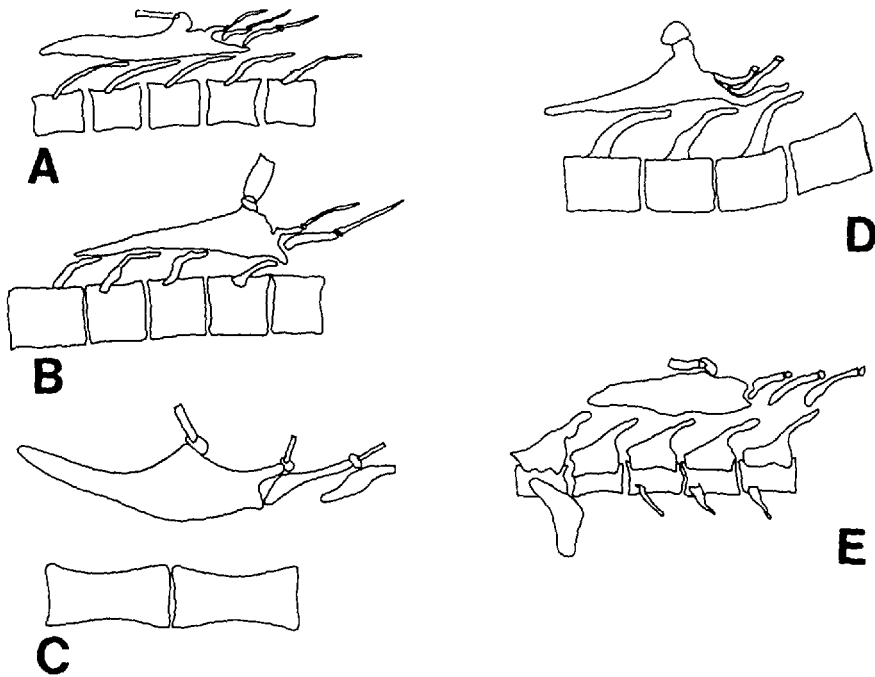


Figure 39. Axial skeleton and vexillar support in A) *Echiodon coheni*, B) *Ec. cryomargarites*, C) *Ec. dawsoni*, D) *Eurypleuron owasianum*, E) *Onuxodon parvibranchium*.

are in the vicinity of vertebrae 4–9 (Table 5). Vexillum position has one derived state: over vertebrae 9–14 in five species of *Echiodon* (Table 5) (71). Anal-fin origin shows no phylogenetic change in position in carapid larvae (in contrast to the adult condition, see above). Adult dorsal-fin origin has one derived state: over vertebrae 9–14 in the same species of *Echiodon* that have a posterior vexillum and in all Carapini. This character has clearly evolved independently since the vexillum of the Carapini remains in the presumably primitive position over vertebrae 4–5 (Table 5). Because the ontogenies of adult dorsal-fin origin are different in the two groups, we consider the ontogeny rather than the dorsal-fin origin itself as the character. Thus, a posteriad adult dorsal-fin adjacent to the vexillum origin is a synapomorphy (72) of some *Echiodon* species and a posteriad adult dorsal-fin origin separated from the vexillum origin is a synapomorphy of Carapini (73).

The final character related to the vexillum is the apparent unique retention of the vexillum in *Echiodon neotes* (74) (see species account).

Relative fin positions may change ontogenetically. In most species no change occurs and fin positions and counts are important clues for resolving species identities. *Pyramodon* and *Onuxodon* are noticeable exceptions. In *Onuxodon*, the A_{30} values in larvae range from 51–55 but are reduced in adults (44–52, Tables 4, 5). The cause of the ontogenetic reduction is not obvious. The possibility that the larval identifications are incorrect is excluded since the diagnostic rocker bone develops precociously by about 4 mm HL. Another example of a change in relative fin position is *Carapus bermudensis* which shows a decrease in VAO and increase in ARDO values (Tables 4, 5). This change clearly involves an anterior, ontogenetic movement of the anal fin origin.

One of our perplexing problems has been our inability to identify larvae of the

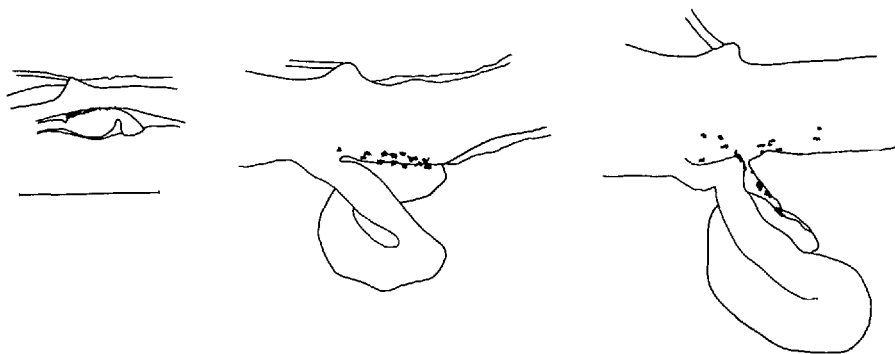


Figure 40. Development of the exterilium gut in *Eurypleuron owasianum*: left = 0.58 mm HL; middle = 1.4 mm HL; right = 1.8 mm HL. All specimens CSIRO uncat.

more apomorphic species of *Encheliophis*. Trott's (1970) specimen of a larval *En. vermicularis* is in poor shape and was cleared and stained for re-examination. We determined that it was *En. dubius* (see *En. dubius* section). The probable basis for Trott's (1970) misidentification was damaged and barely visible pectoral-fin rays; however, all known carapid larvae have pectoral fins. Larvae of one of these species of *Encheliophis* (*vermicularis*) should be identified in eastern Pacific material since the only possible confusion would be with *En. dubius* and VDO values are non-overlapping (16–19 vs. 11–13, Table 4). Despite extensive collections in the region, we have been unable to find specimens or verifiable reports of *En. vermicularis* larvae. The possibility remains that a posteriad migration of the dorsal fin might occur during ontogeny and complicate identification. *Carapus* larvae have been identified to species in the Atlantic where *Encheliophis* does not occur (Olney and Markle, 1979). All *Carapus*-like larvae in the Indo-Pacific are, therefore, considered as *Carapus/Encheliophis*, unless counts and distribution can be used as with Trott's specimen.

Two additional characters associated with ontogenetic change are found in the echiodontines. In *Echiodon coheni*, there are precocious vomerine fangs (75) (see species account) and *Ec. dawsoni* and *Ec.* unnamed larvae have unusually large eyes (76) (see species accounts).

GUT. A relatively bulbous, sac-like gut may be primitive for carapids; however, the paucity of data on larval morphology in outgroups makes this speculative (Gordon et al., 1984). Two derived states are tentatively identified: a small compact gut in all Carapini (77) and an exterilium gut in *Eurypleuron* (78). The sequence of exterilium formation is depicted in Figure 40. When the straight gut of the smallest larvae begins to form a left-handed loop, the loop drops away from the anus and ventral body profile. In the next phase, the anal segment drops away from the ventral body profile to join the loop (Fig. 40). In the fully developed exterilium, the anus is about midway along the gut sac and retains its position relative to the gut loop. Further lengthening occurs in the gut segment anterior to the loop (Robertson, 1975). The elongate anterior gut section and, to some extent, the loop receives flexible but firm support from ventral processes of the coracoid (Fig. 41). The ventral processes of the coracoid are presumably partially resorbed during metamorphosis.

PIGMENT. Larval pigmentation patterns may hold information of phylogenetic utility but character distribution among disparate taxa is difficult to interpret. For example, the spotted post-anal pattern of *Eurypleuron* (Robertson, 1975; Brow-

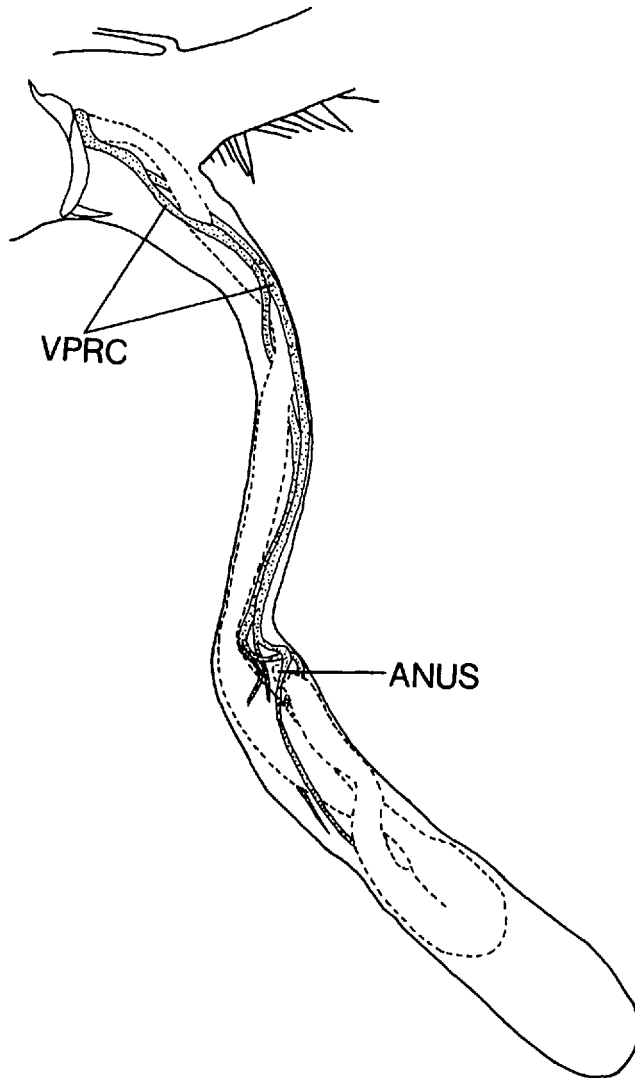


Figure 41. Ventral processes of the coracoid and the exteriorium gut of *Eurypleuron owasianum*, VIMS 8277, 5.5 mm HL.

nell, 1979) is quite similar to that of some ophidiids (*Lepophidium*—Gordon et al., 1984), some gadoids (*Brosme*—Dunn and Matarese, 1984), some lophiiforms (*Lophius*—Fahay, 1983), some pleuronectids (*Eopsetta*—Ahlstrom et al., 1984) and probably several other groups. In the present analysis, we polarize larval pigmentation characters using subfamily outgroups (see Phylogenetic, Reconstruction and Outgroups section) and consider the lateral post-anal spots of *Eurypleuron owasianum* and *Echiodon cryomargarites* (79); the chin spot (Markle and Olney, 1980) of *Snyderidia* (80); and the ring of melanophores around the nasal rosette of known larvae of the Carapini (81) as synapomorphies.

DENTITION. In *Brotula* (Leis and Rennis, 1983), the pyramodontines and *Eurypleuron*, larvae have small, late developing teeth (Figs. 24, 25A). We believe the two derived developmental states represented by the Carapini and *Echiodon* plus *Onuxodon* were characterized sufficiently by the adult arrangements (above).

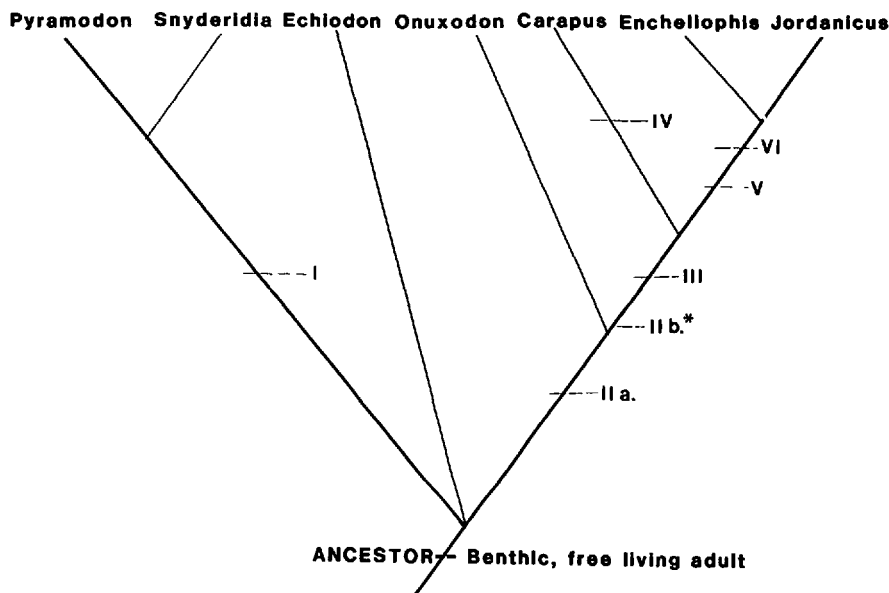


Figure 42. A cladogram of generic relationships based on the eco-behavioral hypotheses of Trott (1970): I. Pelagic adult, II. Adults commensal in a) bivalves or b) holothurians, III. Tenuis stage parasitic, IV. Adults cannibalistic, V. Adults parasitic and VI. Male-female pairing. (*character not representative of all species.)

In the Carapini, premaxillary cardiform teeth (Fig. 27) develop precociously (see species accounts) and are conspicuous. In *Echiodon* (except *Ec. coheni*) and, to a lesser extent, in *Onuxodon*, mandibular fangs and diastema develop precociously (Olney and Markle, 1979 and below). In addition to the absence of precocious mandibular fangs in *Ec. coheni*, larvae are further distinguished by unusual development of vomerine teeth: larvae possess a large recurved canine that is not found in the adult (see species account).

Ecology and Behavior.—One impetus for this study was the opportunity to compare our hypothesis of relationship based on anatomy with an alternate phylogenetic hypothesis of pearlfish evolution put forward by Trott (1970) in his synthesis of pearlfish ecology and behavior. With Dr. Trott's assistance, we have extracted the eco-behavioral data from his paper and attempted a cladistic reconstruction exclusive of any morphological considerations (Fig. 42). The reader should note that Trott used both morphology and eco-behavioral information and, therefore, Figure 42 reflects only a subset of his data.

The starting point of Trott's phylogeny is a benthic free-living ancestor and a (behaviorally) unresolved trichotomy (Fig. 42). The pyramodontines are hypothesized to have pelagic adults; *Echiodon* remains benthic and free living; and other carapids engage in some type of commensalism. The first commensal relationship is with molluscs, which characterizes *Onuxodon* and *Encheliophis dubius* (treated as a *Carapus* by Trott). All other Carapini are holothurian inquiline (one exception—*C. mourlani*) and have a parasitic tenuis stage. *Carapus* spp. are cannibalistic as adults and *Encheliophis* (including *Jordanicus*) are parasites on their hosts and form male-female pairs within their hosts (Fig. 42).

Since 1970, additional observations support or require modest revision of Trott's

hypothesis. Table 6 summarizes literature reports and secondary information we have obtained from museum records and colleagues. Adult habits and microhabitats of *Echiodon* are the most elusive. There are tantalizing bits of information such as nocturnal captures and presence of polychaete worm tubes in trawls (Williams and Shipp, 1982) and anecdotal mention of captures of individuals inside sponges (Ayling and Cox, 1982). Ophidiiforms in general seem to have a propensity for hiding or burrowing in various "substrates," usually inanimate (Svetovidov, 1961). Hiding, whether facultative or obligate, in animate or inanimate substrates, was very likely a propensity possessed by the ancestral carapid. A determination of those "substrates," especially in outer shelf and continental slope forms (pyramodontines, *Eurypleuron* and *Echiodon*), is difficult. The key to using carapid eco-behavioral data in a phylogenetic context is identifying "derived substrates" for hiding. We believe that "invertebrate hosts" is an ill-defined character state. Within the echiodontines, we recognize "molluscan host" as a synapomorphy of *Onuxodon*. Within the Carapini, we recognize "holothurian host" as a synapomorphy of the tribe and its secondary loss as a reversal in *En. dubius*, *C. moulani* and *C. sluiteri*. Clearly, there has been convergence (homoplasy) towards a bivalve host in *Onuxodon* and *En. dubius*. There has been little behavioral or life history work on either taxon and we would expect that their study would be an interesting exercise in microhabitat convergence. Viewed in light of our cladogram (below), "invertebrate hosts" could be a carapine synapomorphy only if one accepts its independent loss in *Eurypleuron* and *Echiodon*.

Observations on host entry behavior may also prove to be of some phylogenetic significance but such data are sparse. Grove and Lavenberg (in press) mentioned some reports of head entry behavior of *Carapus bermudensis* into its common Atlantic host *Actinopyga agassizi* while Arnold (1953) illustrated tail entry by *C. acus*. Our laboratory observations (by J.E.O. aided by L. Trott) of interactions between an unidentified Hawaiian holothurian and *En. gracilis* reveal tail entry. During a short observational period in aquaria at the University of Hawaii Coconut Grove Laboratory, *En. gracilis* was seen to initially locate the host's anus headfirst and then track its caudal tip laterally along the midline to direct the tail into the opening. The specimen then abruptly turned to work itself into the host backwards.

The final datum relevant to phylogenetic analysis is the virtually unprecedented evolution of vertebrate parasites in some species of *Encheliophis* (Trott, 1970, and discussion of relationships of genera below).

RELATIONSHIPS

The ophidiiforms are a diverse, complex and poorly understood group of fishes (Cohen and Nielsen, 1978) whose monophyly has been questioned by Patterson and Rosen (1989) and Markle (1989). We have examined representatives of several major ophidiiform lines and found diversity and complexity of morphological structure. If in fact related to the rest, *Brotula* consistently appears as the sister group of all others while carapids do not appear to form an obvious sister group with any of the others. A number of characters that we interpret as synapomorphies for Carapidae could indicate relationships with other groups. In the interest of completeness we will mention these characters and their implications, should additional study provide corroboration.

An extra pectoral radial, the homology of which is uncertain (either expanded distal radial or fifth proximal radial), is found in carapids, lophiiforms and batrachoidids (Rosen and Patterson, 1969). In our material of *Opsanus* (batrachoidid),

Table 6. Reported hosts of pearlfishes (Abbreviations used are: A—Asteroidea, ASC—Ascidacea, B—Bivalvia; all other host species are holothurians)

Species	Host	Source
<i>C. acus</i>	<i>Holothuria tubulosa</i> <i>Holothuria polii</i> <i>Holothuria</i> sp. <i>Stichopus regalis</i>	Arnold, 1956, Gustato et al., 1979 Gustato et al., 1979 Gustato et al., 1979 Arnold, 1956
<i>C. bermudensis</i>	<i>Actinopyga agassizi</i> <i>Thone</i> spp. <i>Isostichopus badionotus</i> <i>Astichopus multifidus</i> <i>Holothuria glaberrima</i> <i>Holothuria princeps</i> <i>Holothuria lentiginosa</i> <i>Holothuria mexicana</i> <i>Theelothuria princeps</i>	Smith et al., 1981 Ancona-Lopez, 1956 Smith and Tyler, 1969 Trott, 1970 Trott, 1970 Dawson, 1971; Haburay et al., 1974 Miller and Pawson, 1978 Valentine and Goeke, 1983 Trott, 1970 Haburay et al., 1974
<i>C. mourlani</i>	(A) <i>Culcita novaeguineae</i> (A) <i>Pentaceros hawaiiensis</i> (A) <i>Choriaster granulatus</i> (A) <i>Acanthaster planci</i> <i>Stichopus variegatus</i> <i>Stichopus choronotus</i> <i>Bahadshia argus</i> <i>Actinopyga muritiana</i> <i>Holothuria scabra</i>	Mortensen, 1923; Petit, 1934, Schultz, 1960; Smith, 1964; Trott, 1970; Trott and Trott, 1972; Meyer-Rochow, 1977 This study This study Cheney, 1973 This study This study This study, Meyer-Rochow, 1977 This study This study
<i>C. sluiteri</i>	(ASC) <i>Styela aurata</i>	Weber, 1913
<i>En. homei</i>	<i>Bohadschia argus</i> <i>Stichopus chloronotus</i> <i>Stichopus variegatus</i> <i>Thelenota ananas</i> <i>Actinopyga echinites</i> <i>Holothuria argus</i>	This study Smith, 1964, Trott and Garth, 1970, Trott and Trott, 1972, This study Trott, 1970 This study This study Trott, 1970; This study
<i>En. dubius</i>	(B) <i>Pinctada mazatlanica</i> (B) <i>Laevicardium elatum</i> (B) <i>Pinna rugosa</i>	Putnam, 1874; Gunther, 1886; Stearns, 1887; Nelson, 1928 This study This study
<i>En. vermicularis</i>	<i>Holothuria leucospilota</i> <i>Holothuria scabra</i> <i>Holothuria lubrica</i> <i>Thelenota ananas</i>	Masuda et al., 1984 Murdy and Cowan, 1980 Steinbeck and Ricketts, 1941 This study
<i>En. gracilis</i>	<i>Thelenota ananas</i> <i>Actinopyga crassa</i> <i>Bohadshia vitiensis</i> <i>Bohadshia argus</i> <i>Stichopus</i> sp.	This study This study This study This study This study
<i>En. sagamianus</i>	unidentified holothurian	Tanaka, 1908
<i>En. vermiops</i>	Unknown burrowing holothurian	This study
<i>En. boraborensis</i>	<i>Thelenota ananas</i> <i>Bohadschia argus</i> <i>Stichopus chloronotus</i>	This study This study This study
<i>Onuxodon fowleri</i>	(B) <i>Pteria</i> (B) <i>Avicula</i> (B) "pearl oyster"	This study This study This study

Table 6. Continued

Species	Host	Source
	(B) "zigzag lip oyster"	This study
	(B) "clam"	This study
	<i>Bohadschia argus</i>	This study
	<i>Thelenota ananas</i>	This study
<i>O. margaritiferae</i>	(B) "pearl oyster"	This study
<i>O. parvibrachium</i>	(B) "pearl oyster"	This study
	(B) "clam"	This study
	(B) "zig-zag lip oyster"	This study

the radial is ossified and it is not clear that it is a distal radial homologue. In a number of lophiiforms the pectoral radials are greatly elongate, modified and the expanded distal or fifth proximal radial, if primitively present, has been lost (e.g., in our material of *Lophius*). Paracanthopterygian pectoral radials clearly require more detailed study.

A highly modified, elongate first dorsal ray is typical of lophiiforms and carapids. Histological study of such rays, as suggested by Govoni et al. (1984), is needed to ascertain homology.

Eggs shed in a mucilaginous raft are characteristic of carapids (see above) and lophiiforms (Pietsch, 1984).

A foreshortened first epibranchial is characteristic of batrachoidiforms, lophiiforms (Rosen, 1985) and Carapini.

These few characters, in need of further study, suggest that carapids might be related to batrachoidiforms and/or lophiiforms. This would further suggest that similarities with other ophidiiforms are based on shared primitive features. In contrast, Patterson and Rosen (1989) present arguments that would place carapids with ophidiids.

Cladogram.—Our cladogram (Fig. 43) has a consistency index of 0.848. It is one of 12 equally parsimonious trees produced when taxa were grouped to eliminate redundancy and autapomorphies. The variation is due to six trees that place *Snyderidia* as a sister group of *Pyramodon ventralis* rather than of all *Pyramodon* and six trees that place one or more species of *Carapus* as the sister group of *Encheliopsis* (that is, *Carapus* is paraphyletic and *Encheliopsis* is monophyletic). Our reasons for selecting the cladogram (Fig. 43) and, in the two cases just mentioned, for selecting one of two equally parsimonious alternatives, are explained in the following sections in which we discuss the characters associated with major nodes.

Carapidae.—Monophyly of carapids is supported by six synapomorphies, none requiring subsequent reversal. The synapomorphies involve changes in relative fin position (18), the pectoral girdle (21, 28), cheek and jaws (51, 56), and larvae (68). Equally parsimonious cases can be made for considering loss of pelvic fins (39) or greater than 15 PCV (11) as carapid synapomorphies with *Pyramodon* showing re-acquisition of pelvic fins or atavistic reversal in precaudal vertebral number in *Snyderidia canina* and *P. ventralis*. With respect to the pelvic fin, we consider two losses conceptually simpler than one loss coupled to *de novo* re-acquisition. With regard to precaudal vertebral number, we chose the hypothesis requiring one reversal (in *P. ventralis*) rather than two. The cladogram is unaffected by either interpretation.

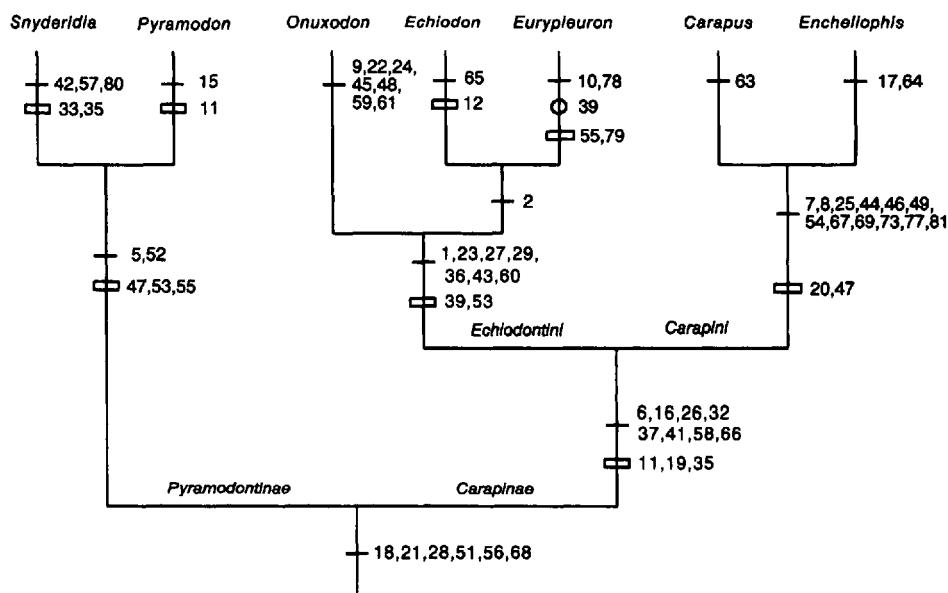


Figure 43. A cladogram of generic relationships in the family Carapidae. Dashes indicate uniquely derived, non-homoplastic characters. Open rectangles indicate homoplasies and open circles indicate reversals. Numerals refer to character states described in the text.

Pyramodontinae.—Five synapomorphies (5—the enlarged ventral facet on the third centrum that receives the retractor dorsalis muscle, 47—round ethmoid, 52—ossified rostral cartilage, 53—fangs at jaw symphyses, and 55—loss of coronomeckelian) define the subfamily *Pyramodontinae* (Fig. 43) as the sister group of the *Carapinae*. Three of these characters (47, 53 and 55) are homoplastic, being found elsewhere in the echiodontines or the Carapini. We hypothesize independent evolution of a rounded ethmoid (47) in pyramodontines and the Carapini but acknowledge the equally parsimonious alternative of atavistic reversal in echiodontines. Half of the PAUP-generated cladograms included *Snyderidia* as the sister group of *Pyramodon ventralis*. We accepted the equally parsimonious cladogram, which recognizes *Snyderidia* as the sister group of all *Pyramodon*, since it conserves current nomenclature.

Relationships within *Pyramodon* (Fig. 44) are poorly resolved; there is an unresolved trichotomy and the only sister group relationship, between *P. ventralis* and *P. parini*, is based on a homoplastic character, long pectoral-fin rays (33).

Carapinae.—The carapine node is well supported by 12 synapomorphies, three of which are homoplastic (Fig. 43). One of the homoplasies (11) requires subsequent reversal (see *Carapidae* relationships section above) while two (19 and 35) are shared with *Pyramodon ventralis* and *Snyderidia canina*, respectively. The remaining nine synapomorphies reflect changes in axial skeleton (4, 6, 16), pectoral skeleton (26, 32), gill arches (37, 41), the swimbladder (58) and the tenuis growth phase (66). These synapomorphies appear to reflect anatomical changes associated with larval growth as well as with elongation and other modifications of adult body construction apparently adaptive for the inquiline adult life of some taxa.

Both carapine tribes are also well supported by synapomorphies. The echiodontine node is supported by nine synapomorphies, two of which are homoplastic. The loss of teeth on the third basibranchial (39) is shared with five species

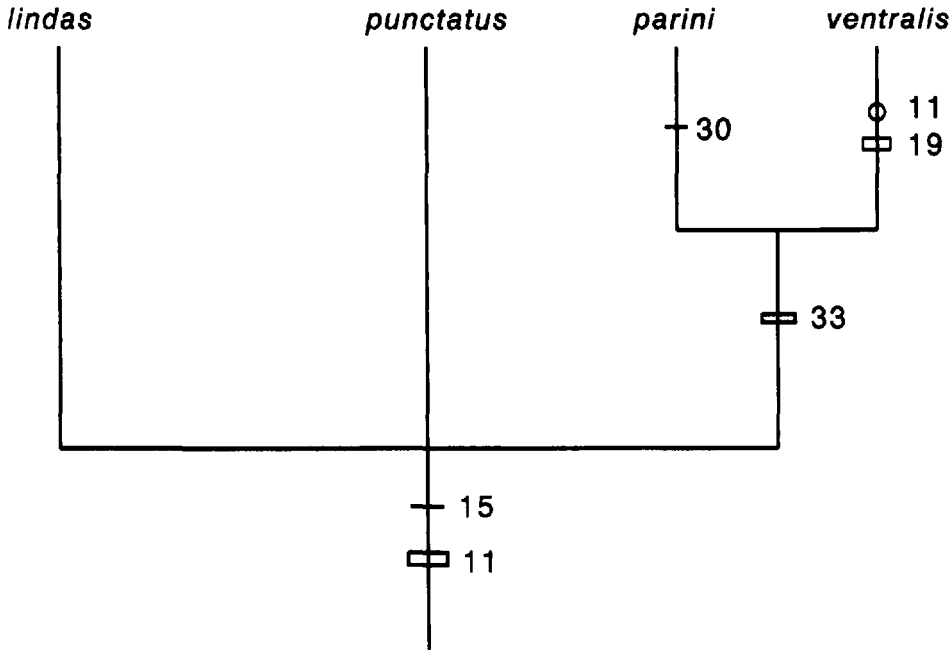


Figure 44. A cladogram of relationships of species in *Pyramodon*. Dashes indicate uniquely derived, non-homoplastic characters. Open rectangles indicate homoplasies and open circles indicate reversals. Numerals refer to character states described in the text.

of *Encheliophis* and reversed in *Eurypleuron*. In addition, we hypothesize that fangs at the jaw symphysis (53) evolved independently in echiodontines and pyramodontines. The other seven echiodontine synapomorphies include changes in axial skeleton (1), pectoral skeleton (23, 27, 29), pelvic skeleton (36), gill arches (43), and swimbladder (60). The carapine node is even more strongly supported with 14 synapomorphies one of which is homoplastic. A rounded ethmoid (47 and see above) evolved independently in pyramodontines. The remaining 12 synapomorphies involve the axial skeleton (7, 8), pectoral skeleton (25), gill arches (44), jaws (46, 49, 54), tenuis growth (67), and larval morphology (69, 73, 77, 81).

Our cladogram as well as Williams' (1984a, 1984b) differs from Trott's (1970) (Fig. 42) in the proposed relationships of *Echiodon* and *Onuxodon*. Trott considers *Echiodon* as a sister group of all other carapines and *Onuxodon* as the sister group of the holothurian inquilines. He explicitly hypothesizes that adult commensalism evolved once, that *Onuxodon* was the first stage in the evolution of commensalism, and that subsequent changes in this character included male-female pairing and parasitism. Two possible revisions to Trott's hypothesis would seem necessary to resolve inquiline evolution with the major, well-resolved nodes of our cladogram: 1) commensalism is a synapomorphy of Carapinae which has been secondarily lost, or not yet discovered, in some echiodontines; or 2) commensalism has evolved independently in both tribes. We lean slightly to the latter in part because two independent acquisitions of inquiline behavior in a group predisposed to hide is not an unreasonable scenario. In addition, we see no need to invoke molluscan commensalism as a precursor to holothurian commensalism. The latter seems a more difficult "housing" arrangement requiring specialized morphology

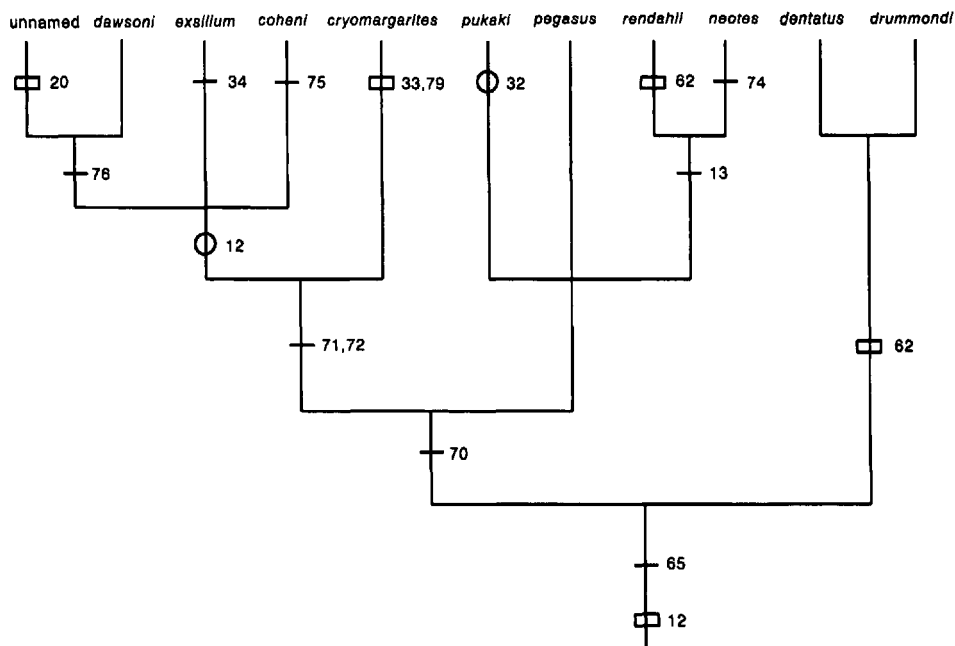


Figure 45. A cladogram of relationships of species in *Echiodon*. Dashes indicate uniquely derived, non-homoplastic characters. Open rectangles indicate homoplasies and open circles indicate reversals. Numerals refer to character states described in the text.

and entry behavior whereas the former is a more common behavior not requiring such specializations. As evidence we note molluscan inquiline are known in tadpole-like liparidids (Able, 1973) and gadid hakes (Markle et al., 1982), as well as *Onuxodon* and *Encheliophis dubius*. No morphological similarity unites these forms, yet all are successful molluscan (bivalve) inquilines. Holothurian inquilinism, on the other hand, is a unique housing arrangement of certain carapines. In contrast to this conclusion, the anecdotal evidence that some species of *Echiodon* may hide in sponges or worm tubes would support the first suggestion. Comparative behavioral studies would be informative.

Points of agreement between us and Trott are in the relationship of pyramodontines and the position of *Encheliophis*. Trott gave no eco-behavioral characters to unite pyramodontines but interpreted adult parasitism as a synapomorphy of *Encheliophis* (sensu stricto: *En. gracilis* and *En. vermicularis*). He also noted Arnold's (1953) mention of juvenile parasitism in *C. acus* (which was based on indirect evidence, apparently missing organs of hosts, rather than direct stomach content evidence) and considered it a precursor to adult parasitism. Our cladogram would change adult parasitism to a synapomorphy of only *En. gracilis* and *En. vermicularis*. Feeding studies of juvenile and adult *En. vermiops*, *En. sagamianus*, *En. boraborensis*, or other Carapini might provide an interesting test of our cladogram and possibly might move the parasite "character" to a lower node on the cladogram.

The *Echiodon* cladogram (Fig. 45) is poorly resolved, and we have little confidence in the details of relationships. The major problems in the genus are rarity (or complete absence) of adult specimens and morphological diversity. Data on larval morphology, though absent in 4 of the 11 species, provides corroboration

Table 7. Frequency distribution of available host records among species of *Carapus* and *Encheliophis* (Data based on this study, surveys of Schultz, 1960; Smith, 1964; Smith and Tyler, 1969; Trott, 1970; Trott and Trott, 1972; Gustato, 1976; Meyer-Rochow, 1977; Smith et al., 1981; and the reports of Tanaka, 1908; Trott and Chan 1972; Weber, 1913)

Species	Holothuria	Asteroidea	Bivalvia	Ascidia
<i>C. acus</i>	59			
<i>C. bermudensis</i>	1,361			
<i>C. mourlani</i>	23	98		
<i>C. sluiteri</i>				1
<i>En. homei</i>	394		1	
<i>En. dubius</i>			5	
<i>En. boraborensis</i>	63			
<i>En. gracilis</i>	66			
<i>En. sagamianus</i>	1			
<i>En. vermiops</i>	1			
<i>En. vermicularis</i>	21			

for some species groupings and is incongruent with others. The larvae of *dawsoni*, unnamed, and *exsilium* are unique as described below. A similar appeal to overall appearance can be made to justify a grouping of three additional larval morphologies: 1) *coheni*; 2) *drummondi*, *dentatus*, *cryomargarites*, *pukaki*, and *pegasus*, and 3) *neotes* and *rendahli* (see species accounts). The *dawsoni* type seems clearly derived to us; it is partly described by characters 71 and 72 features shared by *coheni* and *cryomargarites*. The other larval "forms" are not so easily polarized. The zoogeography of *Echiodon* could inspire additional confidence in this cladogram since many sister taxa tend to be allopatric (see below).

Our rearrangement of generic assignments of some species in the Carapini (Fig. 46) requires comment. As mentioned above, PAUP generated an equal number of trees with a monophyletic *Carapus* and a paraphyletic *Carapus*. Although we would prefer to recognize only well-supported monophyletic taxa, we do not feel that the evidence is yet sufficient and, therefore, have tried to conserve two generic names for these taxa. The genus, *Carapus*, may well be paraphyletic; however, the centrally located swimbladder constriction (63) is unique and found in both sexes of all species within the genus. The classification reassigns the following species from *Carapus* to *Encheliophis*: *homei*, *dubius*, and *boraborensis*. Zoogeographically, there are two consequences to this decision. First, we must hypothesize a Tethyan age to the vicariant event that separated *Carapus* and *Encheliophis*, while elsewhere we hypothesize the same age for the first vicariant event within *Echiodon* (see below). Second, this arrangement appears to have eco-behavioral implications. If a holothurian host is a synapomorphy of Carapini, then "non-holothurian host" is a homoplastic character within *Carapus*. Following Hennig's (1966) logic, homoplasies may indicate characters whose presence is not due to inheritance through common descent. Two species of *Carapus* retain holothurian hosts and are found in the Atlantic while the two species found in the Pacific have "switched" to non-holothurian hosts (Tables 6, 7). As members of the sister group of *Encheliophis*, *C. mourlani* and *C. sluiteri* may have been "forced out" of the holothurian microhabitat by competitively superior *Encheliophis* species, all of which are restricted to the Indo-Pacific. The "non-holothurian host" character of these two *Carapus* may, therefore, be indicative of competitive exclusion rather than phylogeny. Although the above is highly speculative, it can be pointed out that *C. mourlani* does use holothurian hosts on occasion (Table 6), thus allowing

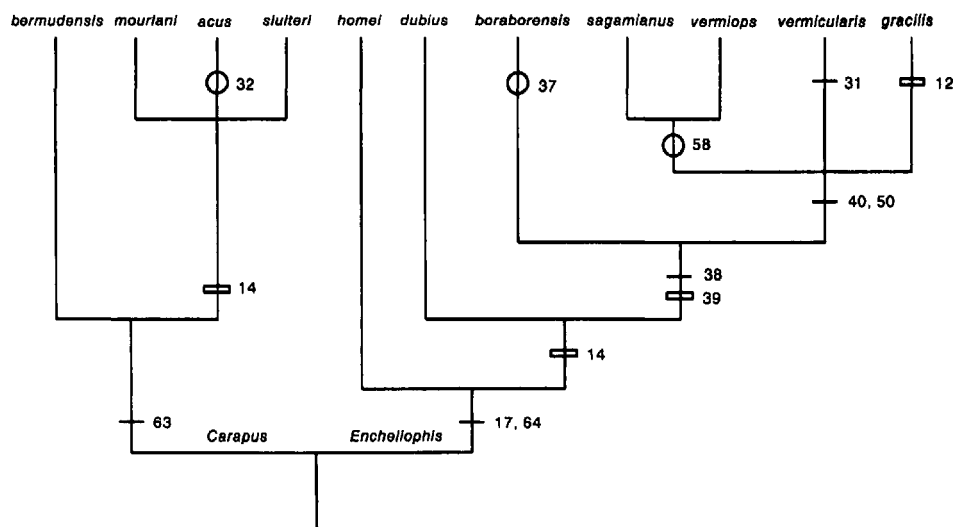


Figure 46. A cladogram of relationships of species in Carapini. Dashes indicate uniquely derived, non-homoplastic characters. Open rectangles indicate homoplasies and open circles indicate reversals. Numerals refer to character states described in the text.

experimental ecologists the opportunity to test habitat preference and competitive exclusion in *C. mourlani*.

KEY TO THE SPECIES OF CARAPIDAE (ADULTS)

- 1a. Pelvic fins present 2
- 1b. Pelvic fins absent 5
- 2a. Margins of dorsal and anal fins edged in black over entire length; head and body generally with few melanophores—central area of cheek unpigmented and pectoral base unpigmented except in largest individuals; P₁ 22–23, DRAO 11–18 *Pyramodon lindas* new species
- 2b. Margins of dorsal and anal fins without black edge or only with posterior quarter pigmented; head and body lightly to darkly pigmented—central area of cheek and pectoral base always pigmented; P₁ 24–30, DRAO 0–12 and/or ARDO 0–5 3
- 3a. Body darkly pigmented but dorsal and anal fins without marginal pigmentation; P₁ 28–30, VAO 9–11 *Pyramodon parini* new species
- 3b. Body usually lightly pigmented, posterior dorsal and anal fin margins may be pigmented over one quarter of their lengths; P₁ 24–28, VAO 5–10 4
- 4a. P₁ 24–26, PCV 14–15, DRAO 0–4 and/or ARDO 0–5, VAO 5–8, snout to anus 0.99–1.33 HL *Pyramodon ventralis*
- 4b. P₁ 26–28, PCV 17–19, DRAO 3–10, VAO 8–10, snout to anus 1.30–1.51 HL *Pyramodon punctatus*
- 5a. Dorsal fin origin anterior to anal fin origin, P₁ 24–27, PCV 13–15, DRAO 6–11 *Snyderidia canina*
- 5b. Dorsal fin origin over or posterior to anal fin origin, P₁ 0–26, PCV 15–35, DRAO 0 6
- 6a. Upper and lower jaw with one to several large, symphyseal fangs, cardiform teeth absent 7
- 6b. Upper and lower jaws lacking enlarged fangs, cardiform teeth present 21
- 7a. Conspicuous tunic ridges on ventral or lateral aspect of posterior swimbladder (Fig. 35) 8
- 7b. No tunic ridges on ventral or lateral aspect of posterior swimbladder 18
- 8a. ARDO 0–7 9
- 8b. ARDO 8–19 13
- 9a. PCV greater than 30 10
- 9b. PCV less than 30 11
- 10a. P₁ 19–20, A₃₀ 47, D₃₀ 38, tunic ridges lateral to the ventral midline, vexillum present *Echiodon neotes* sp. nov.
- 10b. P₁ 14–17, A₃₀ 37–38, D₃₀ 40–43, tunic ridges on ventral midline *Echiodon rendahli*

11a.	D ₃₀ 42–47, tunic ridges on ventral midline, Atlantic Ocean to Mediterranean Sea	12
11b.	D ₃₀ 37, tunic ridges left lateral to the ventral midline, known only from off New Zealand	
	<i>Echiodon pegasus</i> new species	
12a.	Pigmented eye diameter greater than 0.16 HL, North Sea	<i>Echiodon drummondi</i>
12b.	Pigmented eye diameter less than 0.15 HL, Mediterranean and eastern Atlantic	
	<i>Echiodon dentatus</i>	
13a.	P ₁ 26, tunic ridges lateral to ventral midline	<i>Echiodon pukaki</i> new species
13b.	P ₁ 15–21, tunic ridges on ventral midline	14
14a.	D ₃₀ 28–35	15
14b.	D ₃₀ 35–45	16
15a.	A ₃₀ 45–47, VDO 14–15, ARDO 16–19, Indo-west Pacific and Indian oceans	
	<i>Echiodon</i> unnamed	
15b.	A ₃₀ 39–43, VDO 11–13, ARDO 11–12, Atlantic Ocean and Caribbean Sea	
	<i>Echiodon dawsoni</i>	
16a.	PCV 18–20, A ₃₀ 52–54	<i>Echiodon coheni</i>
16b.	PCV 21–29, A ₃₀ 46–50	17
17a.	PCV 21–25, eastern Pacific to Galapagos Is.	<i>Echiodon exsilium</i>
17b.	PCV 25–29, Southern Ocean	<i>Echiodon cryomargarites</i>
18a.	Large median rocker bone associated with anterior swimbladder (Fig. 5), males lack expanded, plate-like parapophyses on thoracic vertebrae, posterior swimbladder embedded in hypaxial musculature	19
18b.	No median rocker bone associated with anterior swimbladder, males with expanded, plate-like parapophyses on thoracic vertebrae (Fig. 59), posterior swimbladder not embedded in hypaxial musculature	<i>Eurypleuron owasianum</i>
19a.	Pectoral fin short (mean 0.24, range 0.16–0.29 HL), horizontal diameter of eyes small (mean 0.13, range 0.08–0.16 HL), precaudal vertebrae 16–18, no lateralis papillae on head or anterior lateral line	<i>Onuxodon parvibrachium</i>
19b.	Pectoral fin long (mean 0.44, range 0.28–0.54 HL), horizontal diameter of eye large (mean 0.18, range 0.15–0.22 HL), precaudal vertebrae 18–22, lateralis papillae on head (especially noticeable on the ventral edge of the interopercle and mandible) and anterior lateral line	20
20a.	Precaudal vertebrae 18–20 (modally 19), relatively short and deep-bodied, mean body depth 0.13 TL (range 0.11–0.16 TL), known only from off western Australia	
	<i>Onuxodon margaritiferae</i>	
20b.	Precaudal vertebrae 19–22 (modally 20), relatively long and slender, mean body depth 0.09 TL (range 0.06–0.10), off South Africa and in Indo-west Pacific to Hawaii	<i>Onuxodon fowleri</i>
21a.	Maxilla wholly or partly adnate	22
21b.	Maxilla free and movable	25
22a.	External pectoral fin visible	23
22b.	External pectoral fin not visible	<i>Encheliophis vermicularis</i>
23a.	Precaudal vertebrae 26 or more; swimbladder long, tubular, extending well beyond vertebra number 12 (Fig. 6B); A ₃₀ 42–52; P ₁ 17–19	<i>Encheliophis gracilis</i>
23b.	Precaudal vertebrae less than 24; swimbladder short, sac-like, not extending beyond vertebra number 12 (Fig. 34); A ₃₀ 39–43; P ₁ 15–16	24
24a.	Dentary and palatine with tightly spaced triangular teeth; PCV 20–22; VDO 16; ARDO 19–20; only known from the southern hemisphere	<i>Encheliophis vermioops</i> new species
24b.	Dentary and palatine with single or double rows of conical teeth; PCV 20–24; VDO 11–14; ARDO 12–18; only known from Japan	<i>Encheliophis sagamiensis</i>
25a.	Swimbladder complex, with a conspicuous midpoint constriction rendering two pseudo-chambers (Fig. 31)	26
25b.	Swimbladder simple, without a midpoint constriction, with one chamber, and with a thin-membrane, pigmented terminal bulb (Fig. 33)	29
26a.	Distributed in Indo-west Pacific from Red Sea to Hawaii	27
26b.	Distributed in Atlantic and Mediterranean	28
27a.	Swimbladder constriction lying under vertebrae 9–10; PCV 15–17; primarily inhabiting species of Asteriodes (starfishes)	<i>Carapus mourlani</i>
27b.	Swimbladder constriction lying under vertebrae 13; PCV 19; exclusively (perhaps) inhabiting species of Ascidiacea (sea squirts)	<i>Carapus sluiteri</i>
28a.	Pectoral fin rays 17–20; distributed along the western shores of the Atlantic Ocean, Bermuda and Caribbean Sea	<i>Carapus bermudensis</i>
28b.	Pectoral fin rays 20–24; distributed along the eastern shores of the Atlantic Ocean and the Mediterranean Sea	<i>Carapus acus</i>
29a.	Pectoral fin small, less than 0.29 HL; entire body highly pigmented; PCV 15–17	<i>Encheliophis boraborensis</i>

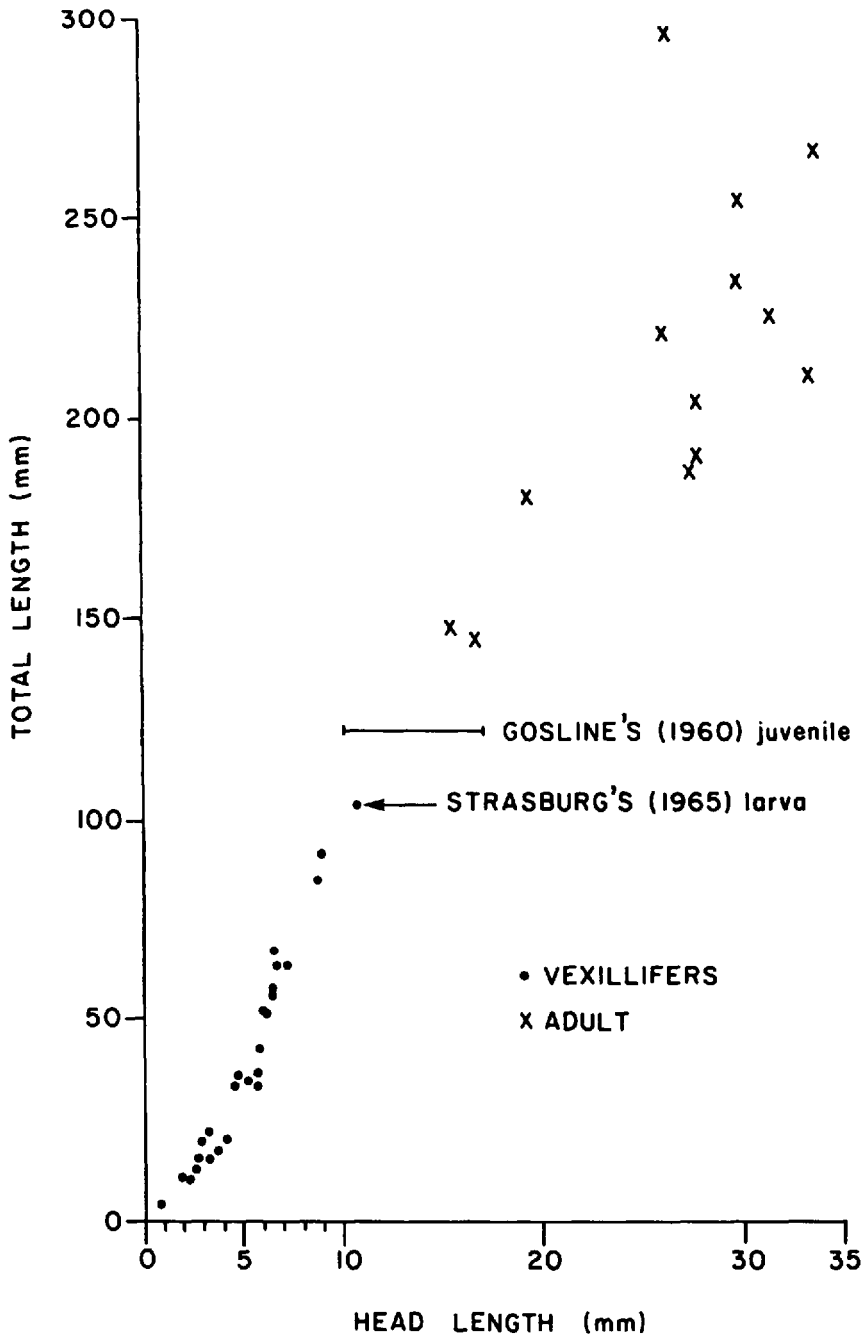


Figure 47. Total length versus head length relationship in *Snyderidia canina*.

Diagnosis: Larvae.—Vexillifer larvae lacking pelvic-fin rays (>2.7 HL), visceral cradle, and cardiform teeth; body not extremely elongate; vexillum placement adjacent to the first dorsal-fin ray and anterior to a vertical through the first anal-fin ray; a simple proximal radial with a wavy ventral contour supports the vexillum

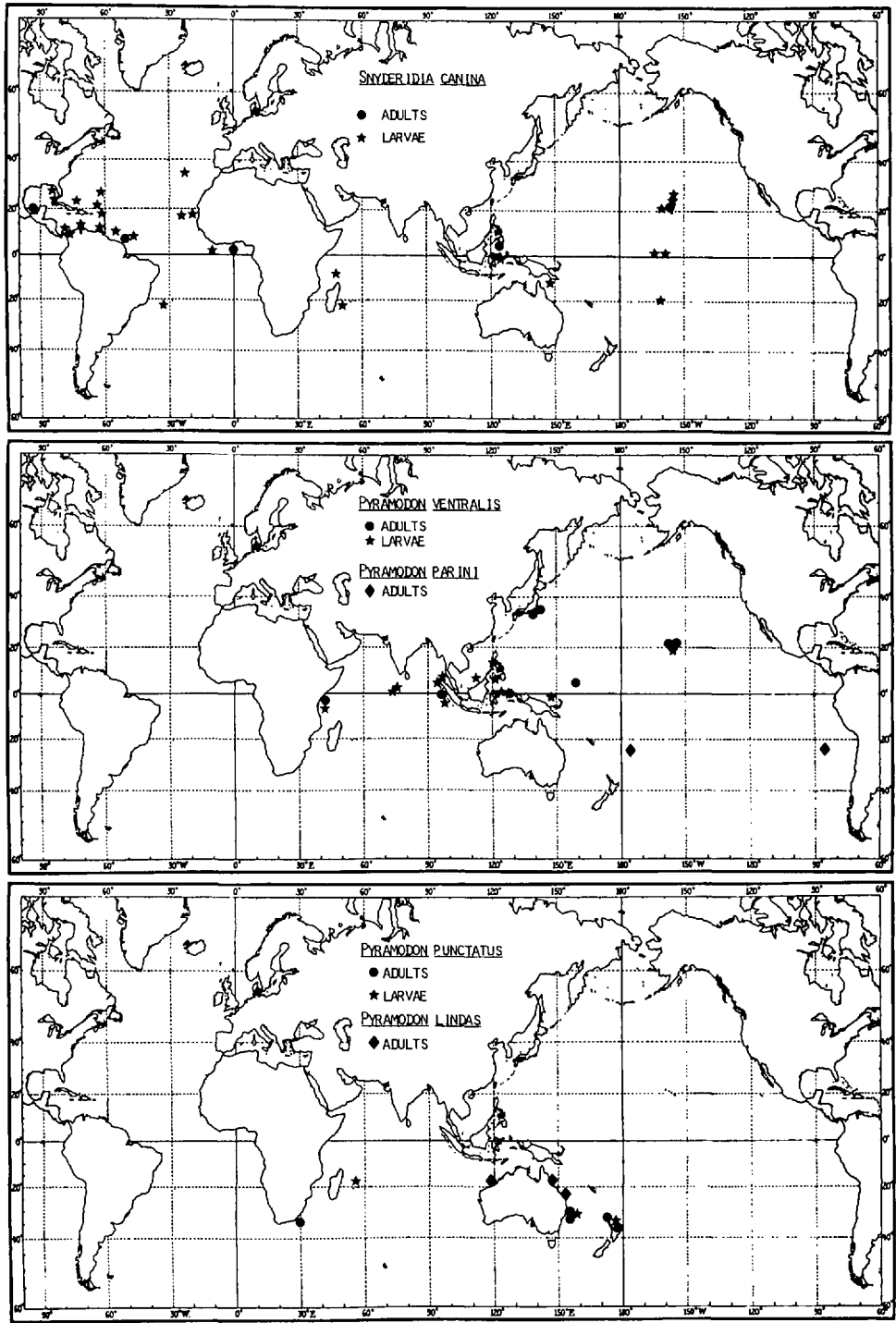


Figure 48. Distribution charts of *Snyderidia* and *Pyramodon*.

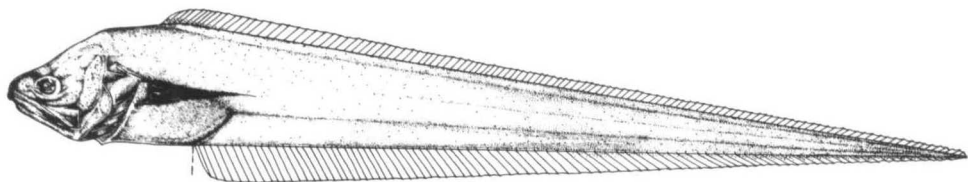


Figure 49. *Snyderidia canina*, USNM 215468, 26.4 mm HL.

and secondarily supports 5–6 dorsal rays; a prominent (in fresh material) concentration of melanophores at the symphysis of the lower jaw; and a large head and deep body (0.34–0.95 as a ratio to HL).

Comments.—The genus is circumtropical (Fig. 48) at depths of about 110 to 1,500 m and is monotypic.

Snyderidia canina Gilbert

Figures 10, 13–15, 17–18, 23, 25, 28, 49–51

Snyderidia canina Gilbert, 1905: 655, pl. 92 (Hawaii).

Snyderidia bothrops Robins and Nielsen, 1970: 287, figs. 2 and 3 (Gulf of Guinea).

Type Material Examined.—*Snyderidia canina* HOLOTYPE, USNM 51646. 33 mm HL (taken from radiograph), 309 mm TL, Station 3989, vicinity of Kauai, 700–909 m. *Snyderidia bothrops* PARATYPE, USNM 201421, 33.3 mm HL, 207 mm TL, vessel LA RAFALE, GTS1, transect 31, sta. 7b/?, 5°06'N, 0°17'W, 260–265 m, 24 September 1963.

Other Material Examined: Adult.—11 lots: Gulf of Mexico, off French Guiana, Gulf of Guinea, Philippines, Hawaii.

Other Material Examined: Larvae.—94 lots: North and South Atlantic, Indian, central and western Pacific.

Description: Adult.—Morphometric and meristic comparisons of Atlantic and Pacific specimens of *S. canina* are presented in Tables 8 and 9 (15.7–33.9 mm HL, 145–268 mm TL). Specimens ($N = 13$) differ slightly in PDL and HW but meristic ranges are indistinguishable. Meristic values of the holotype of *S. canina* (USNM 51646) and a paratype of *S. bothrops* (USNM 201421) are, respectively: A_{30} 46, 44; D_{30} 50, 50; PCV 15, 14; VDO 6, 6; VAO 10, 10; VPB 5–6, 5–6; DRAO 11, 7–8. Values of DRAO vary from 6–11 in our material and to some degree reflect body contortion in preserved specimens. The general appearance of *Snyderidia canina* is depicted in Figure 49. Excellent illustrations and descriptions of type material in Gilbert (1905) and Robins and Nielsen (1970) and an anatomical description by Gosline (1960) should be consulted for further details. The following is a brief summary of external morphology: body ground color in preservative light gray to brown and almost completely concealed by small, round to amorphous, black spots; mouth, gill cavity and peritoneum black; flesh soft; body elongate compressed and tapering; pectoral fin longer than head length; dentition strong with fangs at symphyses of both jaws and on vomer.

Description: Larvae.—Markle and Olney (1980) illustrated and described larval *S. canina* from Pacific localities. Mean, range and standard deviation of morphometrics in 14 larval specimens (2.2–6.9 mm HL, 11–67 mm TL) are as follows (values expressed as a ratio to HL): SNL 0.27, 0.22–0.32, 0.03; ED 0.31, 0.25–0.37, 0.04; UJL 0.60, 0.52–0.73, 0.06; LJL 0.72, 0.59–0.93, 0.10; ML 2.65, 1.67–3.57, 0.66; PVL 1.35, 1.23–1.53, 0.08; PDL 1.44, 1.32–1.67, 0.10; PAL 1.41, 1.24–1.60, 0.06; PL 0.25, 0.20–0.28, 0.03; HD 1.05, 0.76–1.23, 0.15; BD 0.75,

Table 9. Meristic comparisons of Pacific and Atlantic specimens of *Snyderidia canina*

Pectoral rays	N	Atlantic	N	Pacific
	7	25-27	7	25-26
A ₃₀	6	43-46	6	42-46
D ₃₀	6	47-50	5	47-50
PCV	7	14-15	7	13-15
VDO	6	6-7	4	6-7
VAO	5	9-11	6	8-10
DRAO	5	6-8	5	6-11
VPB	2	5-7	1	5-6

0.34-0.95, 0.17. Means and ranges of body proportions of larvae from Atlantic and Pacific localities are almost identical. Ontogenetic trends were noted in measurements of PL and BD with ratios increasing with increasing HL. Other values remained constant throughout the size range examined. Change in total length with head length is gradual to about 5 mm HL, at which point there is a sharp change in slope, and total length increases much faster than head length (Fig. 47). At about 8-10 mm HL the more gradual increase in total length, characteristic of the early stage, resumes (Fig. 47). Meristic values of cleared and stained *S. canina* larvae are reported in Table 5. The general appearance of larvae is shown in Figures 50 and 51.

Diagnoses: Adults and Larvae.—See genus account.

Comments:—Our examination of type and additional material suggests characters used by previous authors (Robins and Nielsen, 1970; Williams 1983) are variable. In a comparison of both nominal species Robins and Nielsen (1970) noted striking similarities in body form and meristics but considered *S. bothrops* as distinct on the basis of having more and stronger teeth, especially multiple rows of posterior dentary teeth. Williams (1983) disagreed with characters of fang size and number but did observe differences in "number of rows of conical teeth behind the dentary," presumably referring to the number of rows of teeth on the posterior part of the dentary. Our examination revealed that the outer row of small teeth is variable and is found in specimens from both areas. In his comparison of *Snyderidia* and *Pyramodon*, Williams (1983) noted a visceral cradle in a single cleared and stained specimen of Atlantic *S. canina* (USNM 214035) and concluded that *Snyderidia* showed retarded development of this structure. Our examination of USNM 214035, and additional material, reveals that the visceral cradle as described by Markle and Olney (1980) is absent in all *Snyderidia*. As mentioned earlier (see Characters and Polarity) we suspect that the elongate, frequently bent or broken anal-fin radials of *Snyderidia* (Fig. 2) caused the misinterpretation.

The geographic distribution of *S. canina* covers the greatest longitudinal range of any species in the family (Fig. 48). The apparent absence of *S. canina* in the eastern tropical Pacific is discussed in the zoogeographic section below. Although Robins and Nielsen (1970) noted that *S. canina* are found in areas "frequented by a variety of large, deep-water holothurians," none has ever been found within a holothurian. The lack of evidence of inquilinism in *S. canina* and other deep water carapids may be a reflection of capture artifact, however we accept this negative evidence for now rather than invoke an unsubstantiated complex behavioral adaptation.

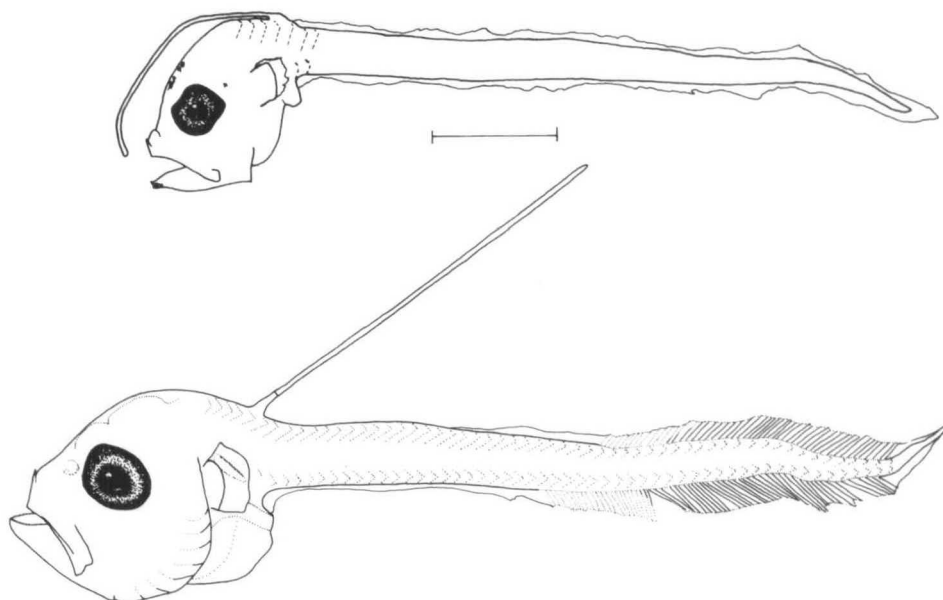


Figure 50. Top: *Snyderidia canina*, GMBL 74-283, 1.0 mm HL. Bottom: *Pyramodon ventralis*, ZMUC DANA 3902", 2.1 mm HL, pelvic fin anlage present but not visible in this view.

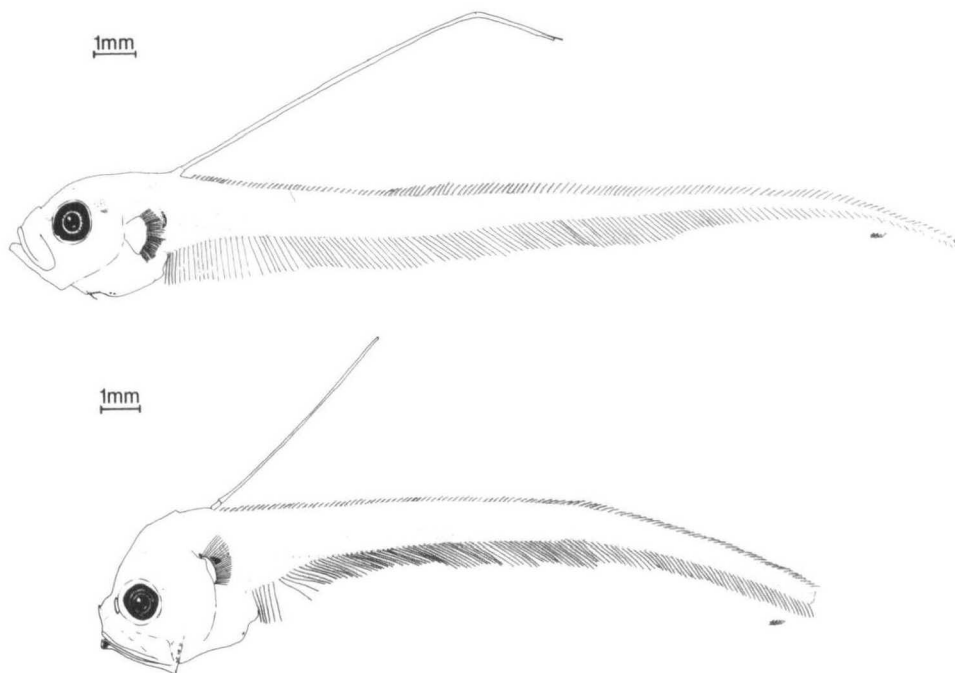


Figure 51. Top: *Pyramodon ventralis*, VIMS 08279, 4.7 mm HL. Bottom: *Snyderidia canina*, MCZ 70074, 5.8 mm HL. Both figures reproduced with permission from Gordon et al. 1984.

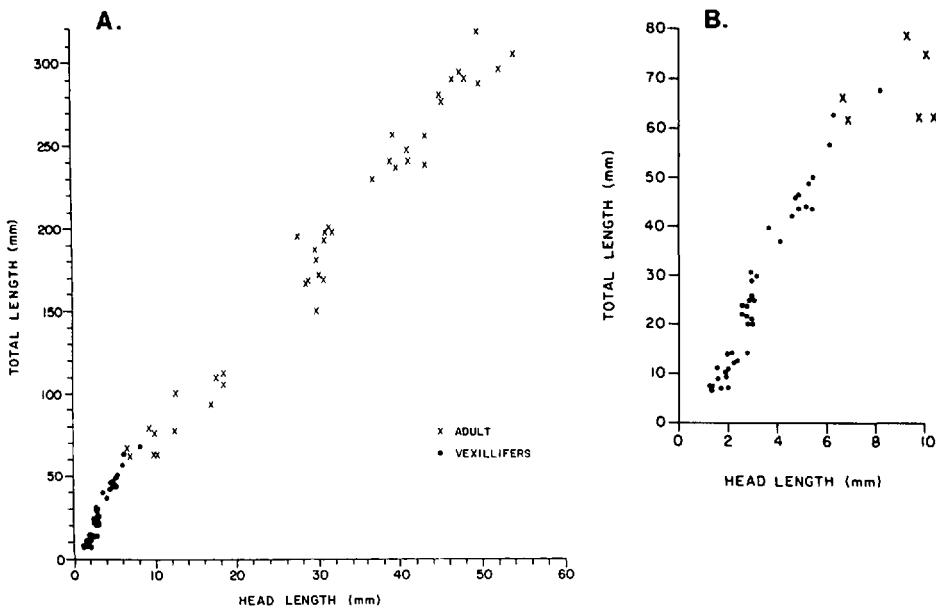


Figure 52. A: Total length versus head length relationship for *Pyramodon* spp. B: Detailed plot of relationship in larvae.

Pyramodon Smith and Radcliffe

Pyramodon Smith and Radcliffe, in Radcliffe, 1913: 175, by original designation).

Cynophidium Regan, 1914: 16 (type species, *Cynophidium punctatum* Regan, 1914: 16, by monotypy).

Growth Stages.—Growth in *Pyramodon* (Fig. 52) appears to follow the same pattern of HL-TL slope changes as identified in *Snyderidia*.

Diagnosis: Adult.—Carapids lacking rockerbones, cardiform teeth, intrinsic swim-bladder constrictions and tunic ridges; possessing pelvic-fin rays, and robust, elongate dorsal- and anal-fin radials; dorsal-fin origin anterior to or directly over the anal-fin origin; swimbladder filling visceral cavity and always reaching past anus; flesh firm; a large, single vomerine fang; cartilaginous interarcual element smaller than the first epibranchial; a large, partly ossified premaxillary cartilage; P_1 22–30, A_{30} 43–53, PCV 14–19, DRAO 0–18, ARDO 0–5, and 3 developed gillrakers; adults reach a large size in all species.

Diagnosis: Larvae.—Vexillifer larvae lacking cardiform teeth, pronounced premaxillary and dentary fangs, and pigment at the symphysis of the lower jaw; body not extremely elongate; vexillum placement adjacent to the first dorsal-fin ray and anterior to or directly over a vertical through the first anal-fin ray; a simple proximal radial with a wavy ventral contour supports the vexillum and secondarily supports 5–6 dorsal rays; elongate anal-fin radials form a visceral cradle; head large and body deep (36–106% HL); and an enlarged premaxillary cartilage present.

Comments.—The geographic distribution of the genus is shown in Figure 48. Species of *Pyramodon* inhabit depths of about 120 to 731 m.



Figure 53A. *Pyramodon lindas*, holotype, AMS I22825-011, 50.9 mm HL, 287 mm TL.

***Pyramodon lindas* new species**
Figures 53A, 53B

Type Material Examined.—HOLOTYPE, AMS I22825-011, 50.9 mm HL, 287 mm TL, female, 18°59'S, 117°10'E, 300–326 m, R/V SOLEA SO2.82.42, 13 April 1982, bottom trawl. PARATYPES, AMS I 22825-029, 2 specimens 36.6–58.5 mm HL, collected with the holotype. QM I18768, 46.8 mm HL, 23°11'S, 153°00'E, 330–385 m, CRAIGMIN, 20 October 1980, trawl.

Other Material Examined.—Adults: AMS I22825, 1 specimen 17.6 mm HL, collected with holotype; QM I15800, 1 adult head and backbone, 30.0 mm HL, 18°03'S, 147°10'E, 320–360 m, 28 February 1979, trawl. Larvae: MCZ 70071, 1 vexillifer 6.7 mm HL, GRH 1045, 12°47'S, 147°40'E 0–2,150 m, 2 December 1981, RMT10.

Diagnosis.—See key to species of carapids.

Description: Adult.—Size varies from 36.6–58.5 mm HL, 229–360 mm TL. This is the largest carapid known to date. Morphometrics are presented in Table 10, measurements of the holotype, in mm, are: TL 287, HL 50.9, SNL 10.7, ED 13.8, UJL 26.7, LJL 28.6, PDL 57.5, PAL 82.8, STA 81.0, PL 34.2, BD 46.7. Meristics are presented in Table 4, those of the holotype are: P₁ 22, A₃₀ 50, D₃₀ 50, PCV 16, VDO 7, VAO 11, DRAO 13. The general appearance of *P. lindas* is depicted in Figure 53. In preservative, adults of this species are lightly colored with the exception of the dorsal- and anal-fin margins which are quite dark (Fig. 53B).

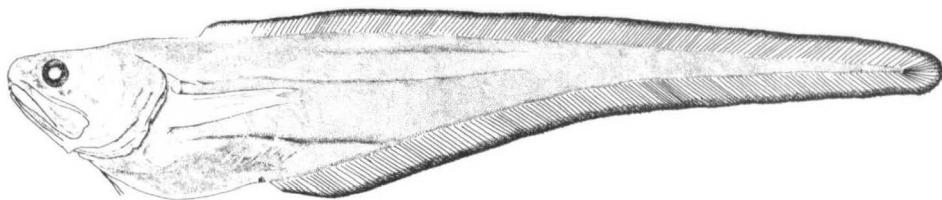


Figure 53B. *Pyramodon lindas*, AMS I22825-029, paratype.

Table 10. Morphometric comparison of adults of four species of *Pyramodon*. Asterisk indicates a specimen with a significant portion of the tail missing

	<i>P. lindas</i>	<i>P. parini</i>	<i>P. ventralis</i>	<i>P. punctatus</i>
HL (mm)	36.6–58.5	12.6–54.4	9.8–44.7	10.3–50.1
TL (mm)	229–360	100–305	79–230*	62–318
SNL	0.2–0.2	0.2–0.2	0.1–0.2	0.2–0.2
ED	0.2–0.2	0.2–0.2	0.2–0.3	0.2–0.3
UJL	0.5–0.5	0.5–0.6	0.5–0.6	0.5–0.5
LJL	0.6–0.6	0.6–0.6	0.5–0.6	0.6–0.6
PDL	1.1–1.2	1.1–1.3	1.1–1.4	1.2–1.3
PAL	1.6–1.7	1.2–1.8	1.0–1.3	1.3–1.5
STA	1.6–1.7	1.2–1.8	1.0–1.3	1.3–1.5
PL	0.7–0.8	0.5–1.1	0.5–1.4	0.6–0.8
BD	0.7–0.9	0.5–0.8	0.7–0.9	0.6–1.0
N	4	13	12	8

There is an unpigmented patch on the cheek that overlies the adductor mandibulae (Fig. 53A). Pectoral fin length is relatively short (Fig. 53B) as in *P. punctatus*, the tips of its rays falling 0–13 mm short of the posterior end of the swimbladder.

Description: Larvae.—Only one larva could be confidently identified as *P. lindas* (probably better described as a pelagic juvenile, though the vexillar proximal segment is still present). The specimen (MCZ 70071., 6.7 mm HL and 66 mm TL) was collected in the same general area off northern Australia (12°47'S, 147°40'E) as the type material, is damaged and has 24 pectoral-fin rays on the right side. The left pectoral fin is missing. Morphometric data, expressed as a ratio to HL, are: SNL 0.27, ED 0.28, UJL 0.59, LJL 0.64, PVL 1.61, PDL 1.75, PAL 1.54, PL 0.29, HD 0.87, and BD 0.90.

Comments.—Our adult material is restricted to the northern coast of Australia from depths of 300–385 m (Fig. 48). Three additional lots of larvae with low pectoral counts were found in Indonesian waters as far north as 08°02'N, 109°37'E. These larvae could be distinguished from sympatric *P. ventralis* if their pectoral development is assumed to be complete, but our material is insufficient to verify the exact size at which pectoral fin development is completed in each species of *Pyramodon*. Four additional lots of small *Pyramodon* larvae were found around 20°S between 160°E and 160°W. Their distribution indicates that they also might be attributable to *P. lindas*, as well as *P. parini* or *P. punctatus*.

Etymology.—In recognition of the mature female holotype and paratypes, we use the anglicized plural of two mature women who supported and endured this project. The name should be treated as a noun in apposition.

Pyramodon parini new species

Figures 3, 8, 54

Pyramodon ventralis: Parin, Golovan, Pakhorukov, Sazonov and Shcherbachev, 1981: 12 (Nazca Ridge).

Pyramodon ventralis: Williams, 1983: 848 (Nazca Ridge).

Type Material Examined.—HOLOTYPE, USNM 231353, 43.5 mm HL, 255 mm TL, a male, R/V IKHTIANDR, sta. 41, 25°40'S, 85°33'W, 185–230 m, 24 September 1979, trawl. PARATYPES, MCZ 70076, 52.7 mm HL, male, R/V PROF. MESYATSEV, 25°41'S, 85°35'W, 320 m, 6 September 1983,

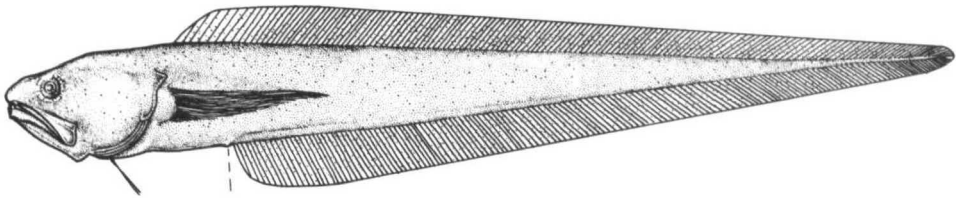


Figure 54. *Pyramodon parini*, USNM 231353, holotype, 43.5 mm HL, 255 mm TL.

trawl. ZIL 45269, 4 specimens 27.8–31.7 mm HL, collected with holotype. USNM 298306, 6 specimens 24.0–54.4 mm HL, R/V PROF. MESYATSEV, 25°41'S, 85°31'W, 285–300 m, 3 September 1983, trawl.

Other Material Examined.—NMNZ P16526, 1 specimen 12.6 mm HL, R/V J. Cook J17/42/76, 25°48'S, 176°30'W, 7 December 1976.

Description: Adult.—Size ranges from 27.8–54.4 mm HL, 169–305 mm TL. Morphometrics are presented in Table 10, measurements of the holotype in mm are: TL 255, HL 43.5, SNL 9.0, ED 6.3, UJL 23.1, LJL 24.0, PDL 49.2, PAL 65.9, STA 63.2, PL 42, BD 27. Meristics are presented in Table 4, those of the holotype are: P_1 30, A_{30} 44, D_{30} 47, PCV 15, VDO 7, VAO 9 or 10, DRAO 7. The general appearance of *P. parini* is illustrated in Figure 54. Adults of *P. parini* are the most darkly pigmented in the genus. The pectoral-fin is relatively long (Fig. 54) as in *P. ventralis*, reaching 13 to 19 mm beyond the posterior end of the swimbladder.

Comments.—Our material comes from two localities in the South Pacific (Fig. 48) from depths of 185–443 m. The type was previously mentioned by Parin et al. (1981) and Williams (1983) who incorrectly reported the TL as 107.8 mm and the SL as 103 mm. The latter report also erred in describing the specimen as a mature female. We also experienced initial difficulty in determining sex in carapids but, as pointed out by Smith, et al. (1981), the female has an unpaired sac-like gonad while the male has paired structures. The holotype of *P. parini* has paired gonads, and we believe it is a male.

Included in the morphometric and meristic summaries is one pelagic juvenile, 12.6 mm HL, that we explicitly exclude from the type series. The specimen was tentatively identified on the basis of its pectoral-fin ray count (29) and number of precaudal vertebrae (16). In addition, it is very darkly pigmented with large dense melanophores over the body except along the dorsal midline. This specimen is also the only one not caught in the Nazca and Sala Y Gomez region. See additional comments on possible larval distribution under *P. lindas* (above).

Etymology.—We take pleasure in naming this species in honor of Dr. N. V. Parin, who independently recognized the distinctiveness of the form during his studies of the Nazca and Sala y Gomez Ridge fauna, in recognition of his many contributions to oceanic ichthyology.

Pyramodon ventralis Smith and Radcliffe Figures 50–51, 55

Pyramodon ventralis Smith and Radcliffe, 1913: 175, pl. 17 (Doworra I., Indonesia).

Type Material Examined.—*Pyramodon ventralis*. HOLOTYPE, USNM 74155, 30.0 mm HL, 181 mm TL (measurements taken from x-ray), 01°00'S, 128°00'E, Doworra Is.

Other Material Examined: Adult.—13 lots: off Kenya, Indonesia, Caroline Is., Japan, Hawaii.

Other Material Examined: Larvae.—20 lots: eastern, central and western Indian, and central and western Pacific.

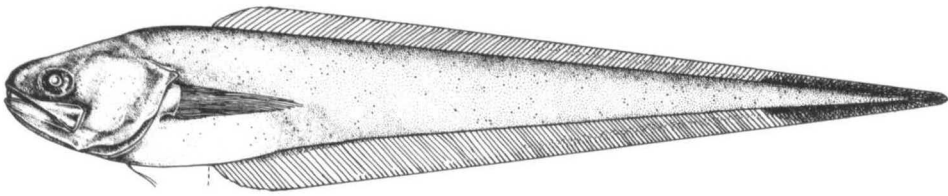


Figure 55. *Pyramodon ventralis*, HUMZ 79559, 38.3 mm HL.

Description: Adult.—Size ranges from 9.8–44.7 mm HL, 62–564 mm TL. Meristics and morphometrics are presented in Tables 4 and 10, respectively. Adults of *P. ventralis* are among the most lightly pigmented in the genus and have a generally more delicate appearance than other species of *Pyramodon*. The pectoral fin is relatively long (Fig. 55), extending 8 to 23 mm beyond the posterior end of the swimbladder. Pectoral-fin length is also strongly allometric, being much shorter than the head length in juveniles and equal to or longer in adults.

Description: Larvae.—Our previous description of *P. ventralis* larvae (Markle and Olney, 1980) was erroneously based on *P. punctatus* larvae (below). Larvae of *P. ventralis* can be identified based on distribution and corroborated in larger specimens by pectoral-fin ray counts (24–26) and anal-fin origin (ARDO 0–5; DRAO 0–4). Morphometric data, expressed as a ratio to HL, for 6 specimens 4.1–6.3 mm HL are: SNL 0.18–0.28, ED 0.26–0.34, UJL 0.49–0.63, LJL 0.60–0.75, VL 3.9–4.7, PVL 1.3–1.5, PDL 1.4–1.6, PAL 1.2–1.4, and BD 0.85–1.06.

Comments.—This species is distributed in the Indo-Pacific from the equator north to about 35°N, at depths of 184–364 m (Fig. 48).

Pyramodon punctatus (Regan)

Figure 56

Cynophidium punctatum Regan, 1914: 16 (New Zealand).

Type Material Examined.—*Cynophidium punctatum*. HOLOTYPE, BMNH 1913.12.4, 29.0 mm HL, 168 mm TL (x-ray only), Terra Nova Exped., 34°25'S, 173°00' E, off Cape North, New Zealand.

Other Material Examined: Adult.—6 lots: off South Africa, New South Wales, Australia, and New Zealand.

Other Material Examined: Larvae.—3 lots: southwestern Indian and southwestern Pacific.

Description: Adult.—Size range 10.3–50.1 mm HL, 62–619 mm TL. Meristics and morphometrics are presented in Tables 4 and 10, respectively. Adults of *P. punctatus* are moderately pigmented. The pectoral fin is relatively short (Fig. 56), the tips of its rays falling 3–10 mm short of the posterior end of the swimbladder.

Description: Larvae.—Only three larger larvae could be confidently identified as *P. punctatus* on the basis of pectoral-fin ray (26–29) and VAO (8) counts and geographic distribution. Two of these specimens had been previously identified by Markle and Olney (1980) as *P. ventralis*. Morphometrics, expressed as a ratio to HL, are: SNL 0.23–0.26, ED 0.26–0.33, UJL 0.45–0.46, LJL 0.52–0.61, VL 1.2–3.5, PVL 1.1–1.6, PDL 1.2–1.6, PAL 1.2–1.9, PL 0.29–0.33, HD 0.63–1.05 and BD 0.82–0.92.

Comments.—*Pyramodon punctatus* is a species inhabiting the southern hemi-



Figure 56. *Pyramodon punctatus*, AMS I19096-005, 47.8 mm HL.

sphere, known from off South Africa, southeastern Australia and New Zealand (Fig. 48) at depths of 120–731 m.

Eurypleuron new genus

Type species, *Carapus owasianus* Matsubara, 1953: 29.

Growth Stages.—Two, corresponding to vexillifer and adult (Fig. 57). There is some evidence of a compensatory tenuis stage in this genus since the largest larva and smallest adult have similar total lengths and greatly different head lengths. It is conceivable that some other growth pattern could account for this observation. Additional material, 8–15 mm HL, is necessary to determine if a tenuis stage is present.

Diagnosis: Adults.—Carapids lacking pelvic fins, rockerbones, cardiform teeth and ventral tunic ridges on the posterior portion of the swimbladder; and possessing thoracic plates formed by expanded parapophyses (transverse processes) on the fifth through 18–20th vertebrae (in males only); dorsal-fin origin over anal-fin origin resulting in equivalent (or almost so) A_{30} and D_{30} values.

Diagnosis: Larvae.—Vexillifer larvae lacking prominent cardiform teeth or enlarged fangs at the jaw tips, enlarged anal-fin radials or visceral cradle; and possessing an exterilium gut supported by elongate, cartilaginous, ventral processes of the coracoid; a vexillum placement slightly anterior to the dorsal- and anal-fin insertion; and a simple proximal radial supporting the vexillum and secondarily supporting dorsal-fin rays 1–3.

Comments.—Gordon et al. (1984) followed Whitley (1941) and Robertson (1975) in identification of the unique exterilium larva (Fig. 61) as *Echiodon rendahli*. None of these authors provided confirmation of the identification, and Olney and Markle (1979) suggested the vexillifer might belong to another carapid genus. The superficial resemblance of the prolapsed condition of the gut of Whitley's holotype with the exterilium of Rendahl's larva captured off New South Wales (Whitley, 1941: 41, fig. 27) may be partially responsible for the original provisional identification. The error has recently been perpetuated by Ayling and Cox (1982) who suggest that the exposed (prolapsed) intestine allows defecation outside a host and reduces risk associated with emergence.

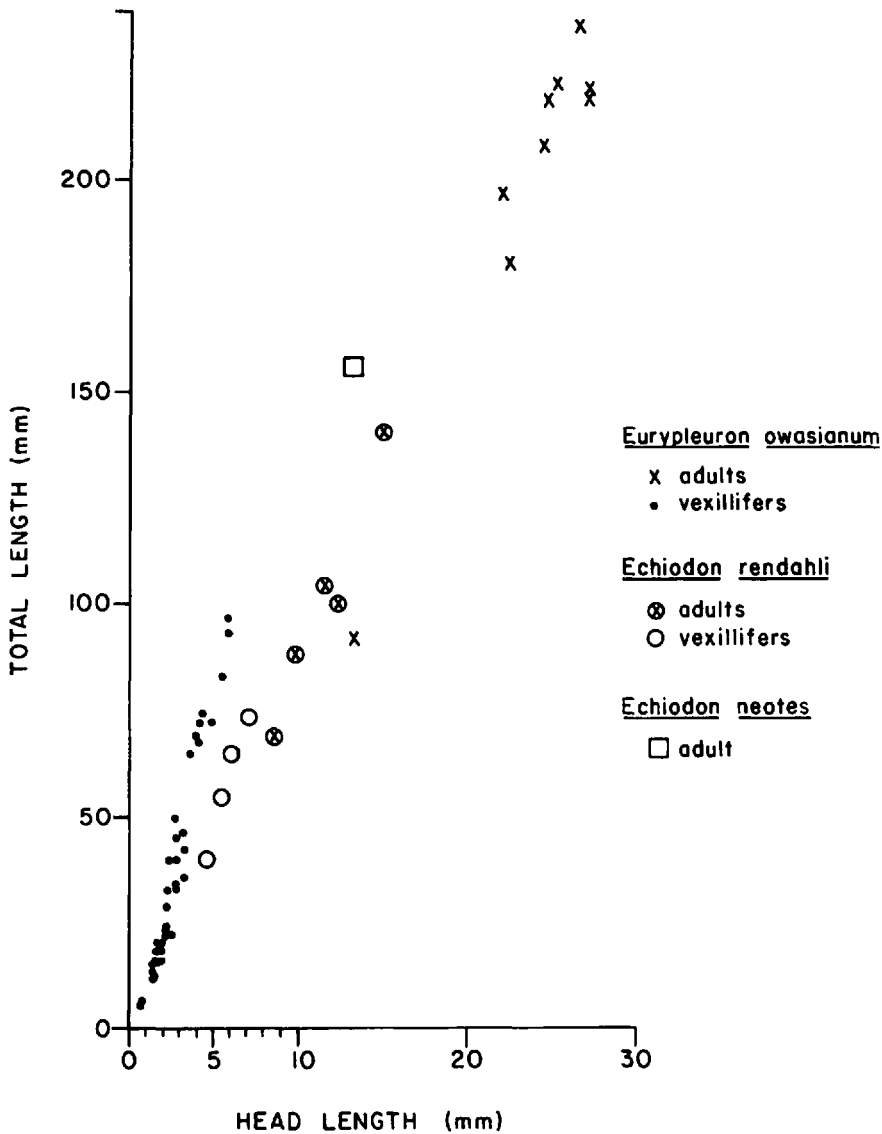


Figure 57. Total length versus head length relationship in *Eurypleuron owasianum*, *Echiodon rendahli*, and *Ec. neotes*.

A number of meristic (Table 5) and anatomical characters delimit the exterilium larva (see Diagnosis). Six echiodontine species are apparently sympatric with *Eurypleuron owasianum*. The genus is monotypic but with three widely separate populations.

The genus is distributed in the Indo-Pacific with a wide latitudinal range and a depth range from the intertidal zone to at least 455 m.

Etymology.—The generic name is a combination of the Greek adjective “eurys” (wide) and neuter noun “pleuron” (rib), in reference to the sexually dimorphic characteristic of males of the genus. Gender is neuter.

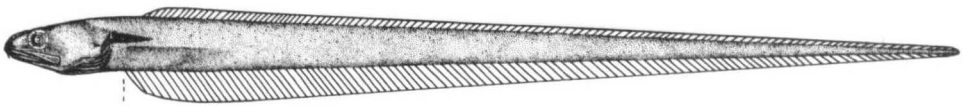


Figure 58. *Eurypleuron owasianum*, AMS 15980-005, 13.1 mm HL.

Eurypleuron owasianum (Matsubara)
Figures 1, 39–41, 58–62

Carapus owasianus Matsubara, 1953: 29, fig. 1 (off Owasi, Japan).

Carapus cinereus Smith, 1955: 409 (Inhaca I., South Africa).

Echiodon rendahli: Robertson, 1975: 405, fig. 1 (New Zealand, larvae).

Echiodon cinereus: Williams, 1984a: 413 (Inhaca I., South Africa).

Echiodon owasianus: Williams, 1984a: 417, fig. 5 (Japan).

Echiodon rendahli: Gordon, Markle and Olney, 1984: fig. 161B (larva).

Type Material Examined. — *Carapus cinereus*, HOLOTYPE, RUSI 309, male, 24.5 mm HL, 215 mm TL, ca. 26°S 33°E, Inhaca Isld., South Africa, deep tide pool, poison.

Other Material Examined: Adult. — 8 lots: southeastern Pacific, off Japan, off southeastern Australia, and off Mozambique.

Other Material Examined: Larvae. — 44 lots: East China Sea, off New Guinea, northern New Zealand, southern Australia, and South Africa.

Description: Adult. — Means, ranges and standard deviation of morphometrics of nine specimens (13.1–27.1 mm HL, 92–236 mm TL) are below. Values are expressed as a ratio to HL and those of Smith's (1955a) type are in parentheses: SNL 0.21, 0.19–0.23, 0.02 (0.21); ED 0.17, 0.14–0.20, 0.02 (0.16); UJL 0.50, 0.49–0.52, 0.02 (0.57); LJL 0.52, 0.51–0.54, 0.01 (0.52); PDL 1.27, 1.21–1.35, 0.05 (1.39); PAL 1.18, 1.06–1.30, 0.08 (1.20); STA 1.09, 1.03–1.19, 0.07 (1.15); PL 0.48, 0.38–0.65, 0.08 (0.56); HD 0.40, 0.36–0.45, 0.03; BD 0.44, 0.38–0.52, 0.05 (0.56); BI 0.12, 0.10–0.14, 0.01 (0.12). Ranges of meristic values are presented in Table 4 and the following values were recorded for Smith's (1955a) type: P₁ 15–16, A₃₀ 39, D₃₀ 42, PCV 25, VDO 7, VAO 5, ARDO 4–5. Although our sample sizes are small, Indo-west Pacific specimens tend to have lower D₃₀ counts (36–42) than specimens from Japan (42–47) or the eastern South Pacific (40–44). The



Figure 59. Positive image of radiograph of *Eurypleuron owasianum*, AMS 16574-003.

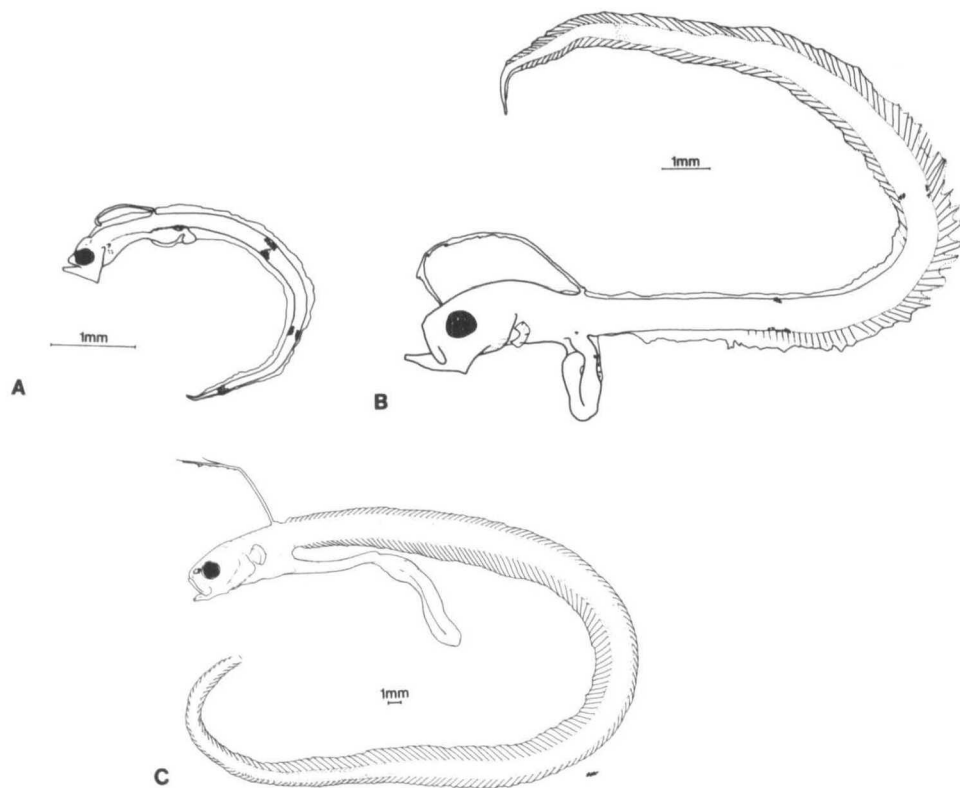


Figure 60. Larval development of *Eurypleuron owasianum*: A) CSIRO uncat., 0.58 mm HL; B) CSIRO uncat., 2.0 mm HL; C) CSIRO uncat., 4.3 mm HL.

general appearance of *Eu. owasianum* is depicted in Figure 58. Smith (1955a) provided a description of color in life. Color in alcohol is cream to dark brown. Small stellate melanophores are liberally scattered over the body but concentrated along the dorsal and anal bases, at the tail tip, and on the cranium and nape.

Description: Larvae.—Size ranges from 0.6–5.7 mm HL, 5.2–93 mm TL. Meristic values of two cleared and stained specimens are presented in Table 5. Larvae have been illustrated and described by Robertson (1975), Gordon et al. (1984), and in some detail herein (Figs. 60, 61). Salient aspects of the development are the large lateral pigment blotches seen in early larvae and the looped, trailing gut (exterilium) that develops by 1.4–2.0 mm HL (Fig. 60).

Comments.—Williams (1984a) re-examined Smith's (1955) holotype of *Carapus cinereus*, noted the presence of expanded parapophyses (transverse processes, Fig. 59) on thoracic vertebrae and commented on the possibility that the character was sexually dimorphic. He considered both *Carapus owasianus* Matsubara, 1953 and *Carapus cinereus* Smith, 1955 to be referable to *Echiodon* but separable on the basis of stomach color and a fleshy snout. A fleshy snout is lacking on Smith's type because the specimen is brittle and in poor condition. In side-by-side comparisons we could detect no difference in snout shape or fleshiness between the FAKU specimens from Japan and IOAN specimens from the eastern South Pacific. We agree that the FAKU specimens have a somewhat more lightly pigmented stomach than the austral specimens.

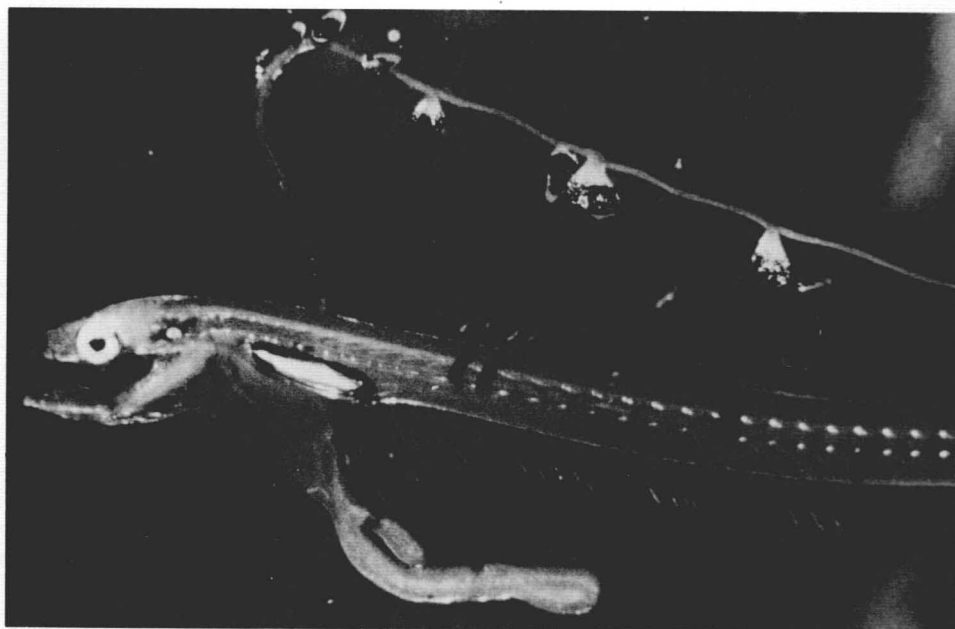


Figure 61. In vivo photograph of *Eurypleuron owasianum*, AMS 22850-001, 4.0 mm HL.

Williams (1984a) did not cite the absence of expanded parapophyses as a character distinguishing *Eu. owasianum* although he reported both male (FAKU 34517) and female material (FAKU 34518, 34519). We have re-examined FAKU 34517 and consider the specimen of indeterminate sex, probably immature (it is the smallest specimens in this collection). All three FAKU specimens lack expanded parapophyses. We have not examined Matsubara's holotype but Williams (pers. comm.) found expanded parapophyses after reexamination of a poor radiograph of that specimen. Additional material from Sala y Gomez Ridge in the southeastern Pacific (Fig. 62), Australia (equal numbers of male and female specimens), the Japanese non-type material (all female or immature) and the type of *Carapus cinereus* (male) lack tunic ridges characteristic of the genus *Echiodon* and help to confirm the sexual dimorphic condition of expanded parapophyses. For example, one collection from Sala y Gomez Ridge (IOAN unregistered, captured 3 May 1987) contains two males (26.5–28.9 mm HL) and one female (28.1 mm HL), and both males have expanded parapophyses while the female does not. We consider the specimens with and without expanded parapophyses as conspecific since there is obvious sexual dimorphism and the forms are otherwise indistinguishable on the basis of morphometric and meristic characters. Differences that do exist are geographic, such as apparent range shifts in precaudal vertebral numbers and stomach color. Because of their teleplanktonic larvae, we are not persuaded that differences detected to date are indicative of more than one species. There is, however, clearly a need for additional material and study.

Echiodon Thompson

Echiodon Thompson, 1837: 55 (type species, *Echiodon drummondi* Thompson 1837: 55, by original designation).

Growth Stages.—Two or three, the tenuis stage apparently variable (Fig. 57 and

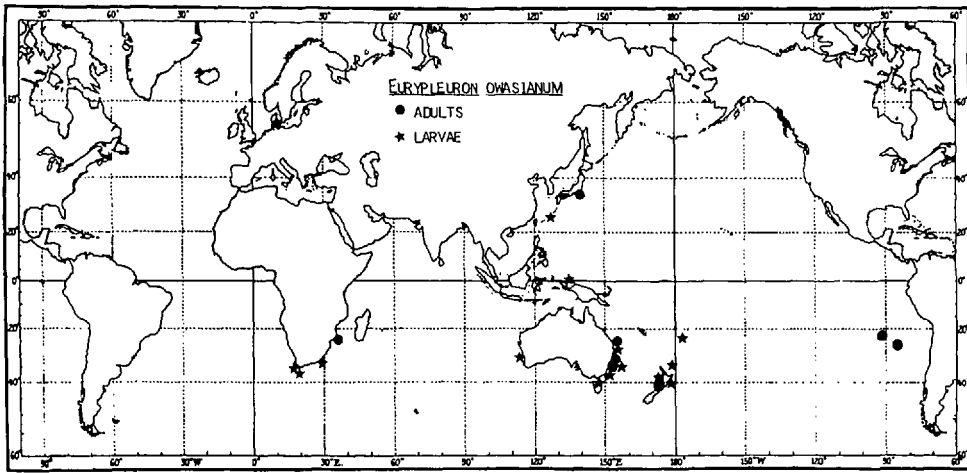


Figure 62. Distribution chart of *Eurypleuron owasianum*.

below). There is no indication of a compensatory tenuis stage in *Ec. rendahli* (Fig. 57) or *Ec. cryomargarites*, but there is in *Ec. dawsoni* and *Ec. exsilium*.

Diagnosis: Adult. — Carapids lacking pelvic fins, rockerbones and cardiform teeth; and possessing a ventral patch of tunic ridges (Fig. 35) on the posterior swim-bladder, numerous small distal radials supporting pectoral rays and one to several large, symphyseal fangs on the dentary and premaxillary.

Diagnosis: Larvae. — Vexillifer larvae lacking ventral fins, rockerbones, cardiform teeth and an extirpium gut; and possessing a vexillum placement just anterior to the first dorsal ray and ranging from directly over to well posteriorad of a vertical through the first anal ray, VVO 7–14, D₃₀ 29–45, VDO 8–15 and ARDO 4–19 (Table 5).

KEY TO THE SPECIES OF *ECHIODON* (LARVAE)

(Some couplets may not be useful in larvae under 2 mm HL)

- | | |
|---|---|
| 1a. ARDO 9–19 | 2 |
| 1b. ARDO less than 8 | 5 |
| 2a. Vexillum inserted over V14, VDO 14–15, ARDO 16–19 | <i>Echiodon</i> unnamed |
| 2b. Vexillum inserted over V 9–11, VDO 9–12, ARDO 9–13 | 3 |
| 3a. A ₃₀ 38, D ₃₀ 29–30, Atlantic Ocean | <i>Ec. dawsoni</i> |
| 3b. A ₃₀ 50–55, D ₃₀ 39–42, Pacific and Indian Ocean | 4 |
| 4a. A ₃₀ 50–51, ARDO 9–11, Eastern Pacific | <i>Ec. exsilium</i> |
| 4b. A ₃₀ 52–55, ARDO 12–14, Indo-west Pacific and Indian Ocean | <i>Ec. coheni</i> |
| 5a. Vexillum inserted over V10, VDO 11, D ₃₀ less than or equal to 40 | |
| | <i>Ec. cryomargarites</i> , <i>Ec. pukaki</i> or <i>Ec. pegasus</i> |
| 5b. Vexillum inserted over V 7–8, VDO 8–9, D ₃₀ greater than or equal to 40 | 6 |
| 6a. A ₃₀ 48–50, D ₃₀ 43–45, North Atlantic to Mediterranean in distribution | 7 |
| 6b. A ₃₀ 45, D ₃₀ 40–41, eastern Australian to New Zealand in distribution | <i>Ec. rendahli</i> |
| 7a. Mediterranean and eastern tropical Atlantic | <i>Ec. dentatus</i> |
| 7b. Eastern North Atlantic and North Sea | <i>Ec. drummondi</i> |

Comments. — *Echiodon* larvae are variable in gut morphology, vexillum placement and support, meristics, pigmentation and dentition. As a result, we have been able to recognize eight of the 11 known species in the genus (Table 5). Larvae tend to fall into two morphological groupings: an *Ec. drummondi*-like morphology

characterized by a pouch-like gut, an anteriorly placed vexillum, a simple radial supporting the vexillum and low ARDO values; and an *Ec. dawsoni*-like morphology that lacks a protruding gut and possesses a posteriorly placed vexillum, a compound radial supporting the vexillum and first dorsal ray and high ARDO values. Larvae of *Ec. cryomargarites*, *Ec. coheni* and *Ec. rendahli* are somewhat intermediate between these two extremes. Larvae of two additional southern ocean species (*Ec. pukaki* and *Ec. pegasus*) are unknown and may be presently confused with larvae of *Ec. cryomargarites*. Despite this variability and potential confusion within the genus, *Echiodon* larvae are distinct and can be delimited from larval *Carapus* on the basis of vexillum placement relative to first dorsal ray; from *Eurypleuron owasianum* by virtue of gut morphology and ARDO values; and from the pyramodontines by a number of meristic, morphometric and osteological characters including D_{30} , MVO (or VVO), ARDO, BD as well as vexillar radial morphology. Vexillifer larvae of *Ec. drummondi* and *Ec. dentatus* are superficially similar to larvae of *Onuxodon* spp. and many meristic values overlap (Table 4). Larvae of these species can be delimited, however, on the basis of vexillum placement (more anterior in *O. parvibrachium* and more posterior in *O. fowleri*), A_{30} values, rockerbone formation in large *Onuxodon* specimens (by 3.5 mm HL) and geographic distribution.

The geographical distributions of *Echiodon* species are presented below. The depth range is from about 18 to 2,000 m.

Echiodon unnamed species
Figures 38, 63

Encheliophis sagamianus: Okiyama, 1986: 333 (larva 27.5 mm TL).

Material Examined: Larvae.—6 lots: East China Sea and North Pacific northeast of Hawaii.

Description: Adult.—Adults of this species are unknown.

Description: Larvae.—A specimen of this species was illustrated in Okiyama (1986) as *En. sagamianus*. Means and ranges of morphometric variables for eight specimens (3.4–4.3 mm HL, 70–100 mm TL) are as follows, all values reported as a ratio to HL: SNL 0.23, 0.20–0.28; ED 0.33, 0.31–0.37; UJL 0.52, 0.47–0.56; LJL 0.59, 0.53–0.62; PVL 2.82, 2.76–3.00; PDL 2.88, 2.80–3.02; PAL 1.54, 1.41–1.51; STA 1.46; 1.41–1.51; HW 0.57, 0.55–0.58; HD 0.68, 0.58–0.82; BD 0.31, 0.29–0.40; LTP 1.08, 1.00–1.21. Ranges of meristic values in six enzyme or formalin cleared specimens are reported in Table 4. The general appearance of vexillifer larvae of this unnamed *Echiodon* species is depicted in Figure 63. External pigment is limited to a few small melanophores scattered over the braincase. Internally, pigment in the form of densely aggregated melanophores is visible along the ventral surface of the hindbrain and on the peritoneum in the posterior portion of the abdominal cavity.

Dentition consists of 1–2 conical teeth at the symphyses of the premaxillae and dentaries separated by a gap from a single row of smaller conical teeth, those of the premaxillae more numerous. A pair of small conical teeth is positioned on either side of the vomer and separated by a space. Palatine bears a single row of sharp villiform teeth.

In two cleared and stained specimens (3.5, 3.9 mm HL, ORI uncata.), transverse processes are developed on thoracic vertebrae 1–3 and are identical in appearance to those described for *Echiodon dawsoni* by Olney and Markle (1979). Vertebral centra appear ossified (react positively to alizarin) throughout the length of the body (except the posteriormost centra), and developing neural spines are visible

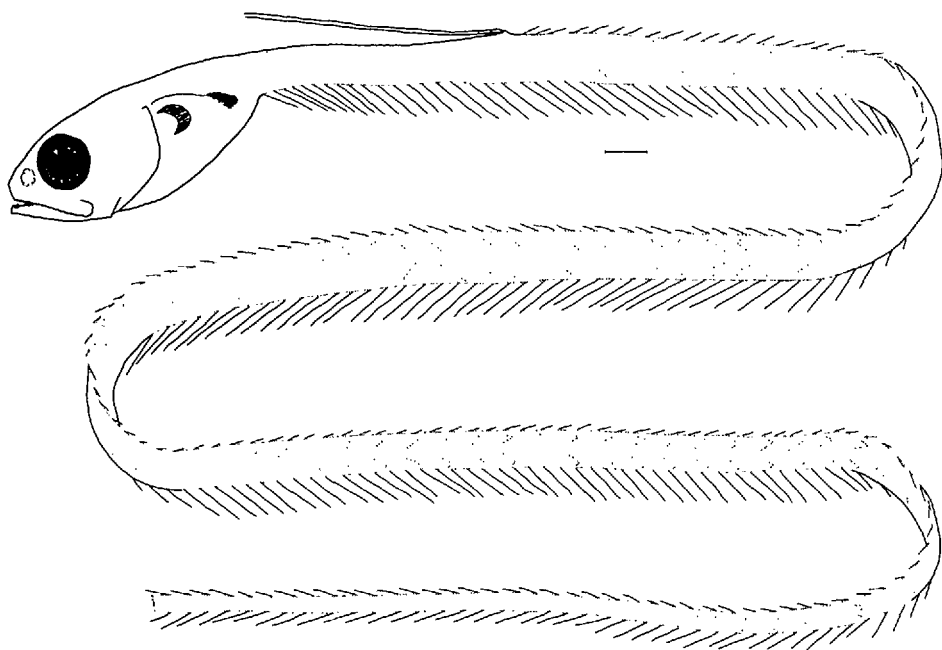


Figure 63. *Echiodon* unnamed, ORIT uncat., 3.7 mm HL.

on vertebrae 1–13. Haemal spines are not developed and number of precaudal vertebrae for this unnamed species is unknown (see Comments). Dorsal- anal- and pectoral-fin rays and supporting elements are fully differentiated and react positively to alcian blue. Only the distal vexillar element appears ossified. The vexillum is supported by a compound, cartilaginous proximal radial (Fig. 38) similar in morphology to that of *Echiodon dawsoni* (Olney and Markle, 1979) and inserts over vertebrae 13–14. A caudal fin is absent.

Diagnosis: Larvae.—*Echiodon* larvae possessing a large eye (ratio to HL, 0.31–0.37); PDL 2.80–3.02 (ratio to HL), a compound radial supporting the vexillum and first dorsal ray, a posteriorly inserted vexillum (VVO 13–14), ARDO 16–19, D_{30} 32–33, A_{30} 45–47 and distributed from the Indian Ocean to the western Pacific off Indo-China.

Comments.—Larvae of this species are not considered referable to *Ec. pukaki* or *Ec. pegasus* on the basis of meristic data (Table 4) and geographical range and can be differentiated from larvae of *Ec. coheni* on the basis of pigmentation, dentition, morphometrics (especially PDL) and meristics (especially D_{30} , VDO and ARDO). It is not surprising that adults of this species are unknown considering the rarity of the apparently allopatric *Ec. coheni*. Based on comparison with its congeners, adults of this unnamed species will likely resemble other small *Echiodon* such as *Ec. dawsoni* and *Ec. exsilium*.

Echiodon pukaki new species

Fig. 64

Type Material Examined.—*Echiodon pukaki*, HOLOTYPE, NMNZ P.16532, 19.0 mm HL, 232 mm TL, male?, R/V WESERMUNDE, W4/174/79, 48°45.03'–43.46'S, 170°25.66'–28.79'E, Pukaki Rise, 857–860 m, 26 Sept. 1979.

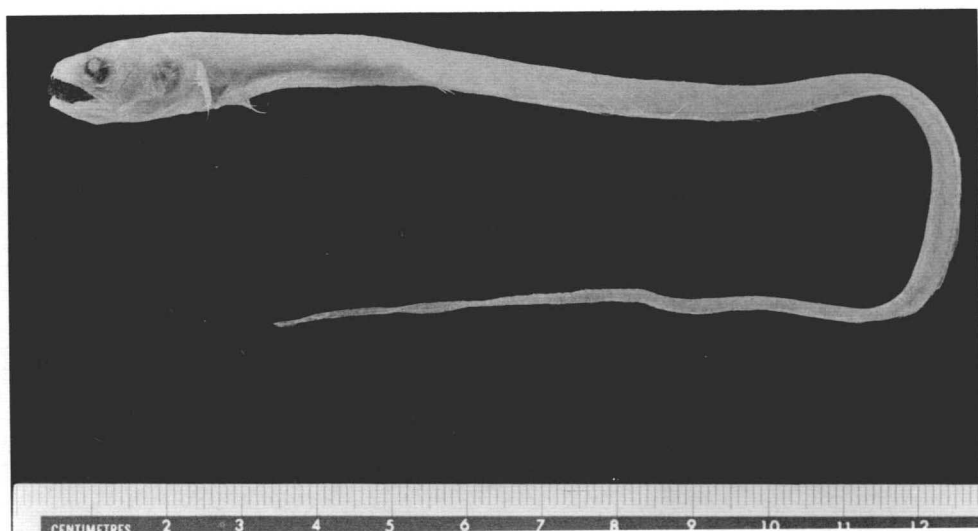


Figure 64. *Echiodon pukaki*, holotype, NMNZ P.16532, 19.0 mm HL.

Description of Type Material. — Morphometry of the holotype expressed as a ratio to HL is as follows, actual measurements (mm) in parentheses: SNL 0.21 (4.0), ED 0.18 (3.5), UJL 0.55 (10.5), LJL 0.55 (10.4), PDL 1.62 (30.8), PAL 1.17 (22.3), STA 1.10 (21.1), PL 0.29 (5.6, distal portions of rays of both fins are damaged), HW .28 (5.4), HD 0.50 (9.6), BI .10 (1.9), LTP 1.08 (20.6). Meristics are presented in Table 4. The general appearance of the holotype (and only known specimen) is depicted in Figure 64. Color in alcohol is tan. Externally, small melanophores are scattered at the tip of the snout and at the nape of the neck. Larger stellate melanophores are densely scattered on the posterior tenth of the caudal portion. These melanophores become subdermal anteriorly and are visible in association with the vertebral column on the posterior half of the caudal portion. Internal melanophores (large and stellate) are scattered on the brain, on the swimbladder and on the abdominal wall dorsal to the swimbladder as well as anteriorly, just behind the pectoral fin base. The stomach and hindgut are black, a portion of which protrudes through the mouth of holotype. Internal melanophores are also visible in series associated with dorsal and anal pterygiophores.

Premaxillary dentition consists of a single, large curved fang (approximately 1.1 mm in length along the anterior edge) followed by considerably smaller, sharp conical teeth which are polyserial, curved inward and extend to the posterior-most tip of the premaxilla. Dentary tooth pattern is similar except the large fang at the lower jaw tip is not as curved and is separated from the following dentary teeth by a diastema (approximately 1.0 mm in extent). The vomer bears four large, conical median teeth surrounded by smaller conical teeth. Palatine teeth are small, stout, almost triangular and polyserial.

The swimbladder is simple, straight and tubular, occupying the anterior half of body cavity and possesses a ventral patch of tunic ridges. The ribs are not expanded.

Description: Larvae. — Larvae of *Ec. pukaki* are unknown but see larval description of *Ec. cryomargarites*.

Diagnosis. — A species of *Echiodon* inhabiting southern oceans and possessing 25–26 pectoral rays, D_{30} 36–38 and ARDO 11.

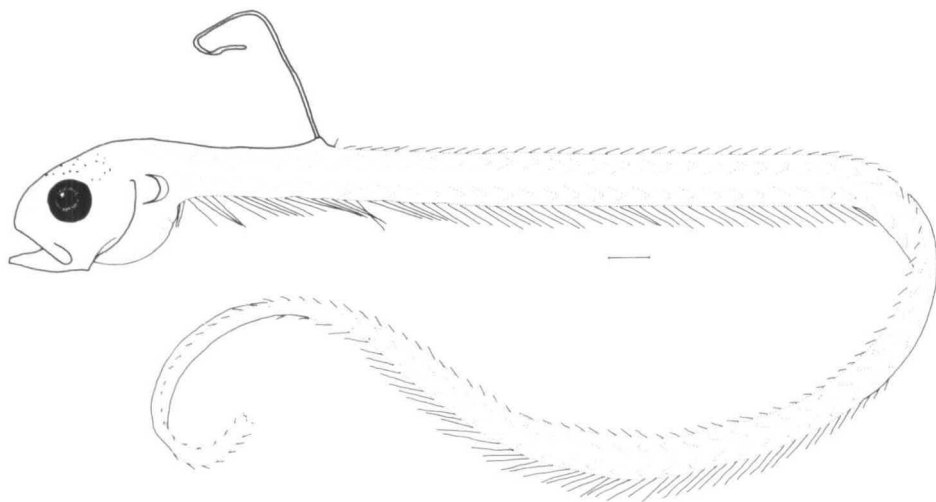


Figure 65. *Echiodon coheni*, ORIT uncat., 3.0 mm HL.

Comments.—Although similar in many respects (geographical distribution, PCV, D_{30} , A_{30} , VDO) to *Ec. cryomargarites*, this single specimen possesses more pectoral fin rays than any known adult carapine and is thus considered a separate species. Additional collections of adults and the identification of larvae referable to *Ec. pukaki* are necessary in order to clarify relationships with *Ec. cryomargarites*.

Etymology.—In reference to the capture locality, Pukaki Rise, the name to be treated as an appositional noun.

Echiodon coheni Williams
Figures 38, 39, 65

Echiodon coheni Williams, 1984a: 415, fig. 3 (Somali).

Echiodon anchipterus Williams, 1984a: 415, fig. 4 (Philippine I.).

Encheliophis sagamianus: Okiyama, 1986 (in part): 333 (larva 77.0 mm TL).

(We note the potential for secondary homonymy of *Ec. coheni* with *Onuxodon coheni* Nolfé, 1980, a fossil taxon in its sister genus.)

Type Material Examined.—*Echiodon coheni*, HOLOTYPE, ANSP 138804, 20.0 mm HL, 143 mm TL, Indian Ocean, Somali, 11°24'N, 51°35'E, 75–175 m, R/V ANTON BRUUN, Cruise 9, Sta. 463; *Echiodon coheni*, PARATYPE, ANSP 150530, 15.0 mm HL, 96 mm TL, collection data same as ANSP 138804; *Echiodon anchipterus*, HOLOTYPE, USNM 258905, 16.1 mm HL, 110 mm TL, Philippine Islds., Visayan Sea between Negros and Masbate Island, southwest of Caduruan Point, 11°35'45"N, 123°55'32"E, 0–78.7 m, trawl.

Other Material Examined.—Larvae: 33 lots from Indo-Pacific localities.

Description: Adults.—Adult material was described and illustrated by Williams (1984a). We note one discrepancy; the holotype possesses 18 PCV. The species is of moderate size, compressed, with a relatively deep body and abrupt rather than gradual taper to the tail.

Description: Larvae.—One larva, 77.0 mm TL, was illustrated in Okiyama (1986) as *En. sagamianus*. Means, ranges and standard deviation of selected morphometrics (expressed as a ratio to HL) in a sample of eight specimens (1.9–5.1 mm HL, 17–74 mm TL) are as follows: SNL 0.27, 0.24–0.29, 0.02; ED 0.30, 0.26–0.32, 0.02; UJL 0.52, 0.44–0.57, 0.05; LJL 0.56, 0.50–0.60, 0.03; PVL 2.00, 1.77–

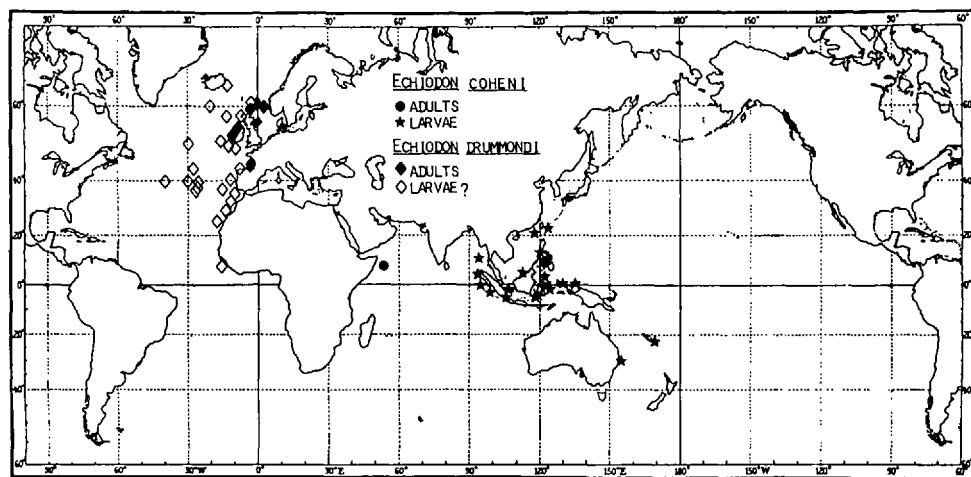


Figure 66. Distribution chart of *Echiodon coheni* and *Ec. drummondii*.

2.19, 0.14; PDL 2.08, 1.82–2.29, 0.16; PAL 1.26, 1.13–1.38, 0.08; HD 0.81, 0.65–0.96, 0.11; BD 0.42, 0.35–0.54, 0.06. Meristic values in seven specimens (one was cleared and stained, the others cleared in foramlin) are reported in Table 5. The general appearance of vexillifers of *Ec. coheni* is depicted in Figure 65. Larvae ranging from 1.4–3.5 mm HL (the majority of our material) are sparsely pigmented with small melanophores scattered (internally and externally) around the brain, snout, nasal rosettes and cranium. In a small specimen (1.9 mm HL), some peritoneal pigment is visible associated with the developing swimbladder. In our two largest specimens (5.1–5.3 mm HL), cephalic pigment is more conspicuous due to an increase in size, density and distribution of melanophores. By 5.3 mm HL, melanophores are scattered over the entire head including the cranium, brain, snout, cheek, upper and lower jaws, vomer and tongue.

Premaxillary, dentary and palatine teeth develop slowly in *Ec. coheni* and are only barely visible in a 5.1 mm HL specimen. Enlarged canines at the tip of the upper and lower jaw, which are characteristic of adults, are not visible in our larval material. The vomer bears a single, large, curved canine in larvae ($N = 5$) ranging in size from 2.9–3.2 mm HL. In the two largest specimens (5.1–5.3 mm HL), this tooth is not present. In the largest specimen, a pair of posteriorly directed, small conical teeth are visible on the vomer. Larvae of intermediate size are not available and we are unable to further clarify this unusual developmental pattern.

In a single cleared and stained specimen (2.9 mm HL), the vexillum inserts over vertebra 10 and is supported by a compound proximal radial that is cartilaginous and secondarily supports the second and third dorsal ray (Figs. 38, 39). The modified radial extends over thoracic vertebrae 8–11. Rays and supporting elements of dorsal and anal fins are fully developed but not ossified. Supporting elements of the pectoral fin are not fully differentiated and pectoral rays are absent. Vertebral centra, neural and haemal spines all appear cartilaginous and the first haemal arch is visible on vertebra 21. Transverse processes are not developed on thoracic vertebrae. A caudal fin is absent.

Diagnosis: Adults.—A species of *Echiodon* with less than 21 PCV and distributed in the west Pacific and Indian Oceans.

Diagnosis: Larvae.—An *Echiodon* larva possessing a compound radial supporting the vexillum and three dorsal rays, VVO 9–10, ARDO 12–14.

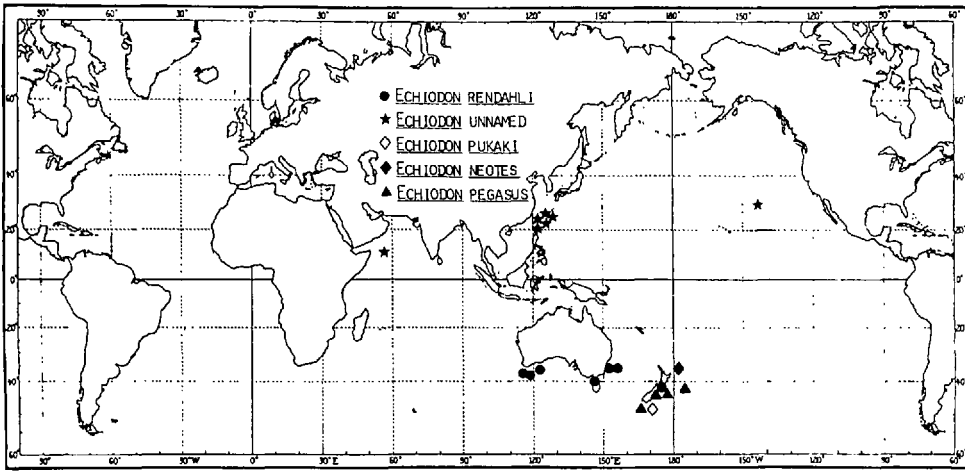


Figure 67. Distribution chart of *Echiodon rendahli*, *Ec. unnamed*, *Ec. pukaki*, *Ec. neotes*, and *Ec. pegasus*.

Comments.—Our identification of larvae is based solely on their possession of two meristic characters, A_{30} 52–55 and PCV 19–20, both of which are unique among species of *Echiodon* (Table 4). Williams (1984a) distinguished *Ec. coheni* and *Ec. anchipterus* on the basis of pectoral ray and D_{30} counts. He predicted that the difference in D_{30} values would vanish when variation for the character was better known and that these taxa would be shown to represent allopatric species. No additional adult material is available. As a result, our larval data are crucial to the allocation of these two nominal forms. The data support Williams' (1984a) prediction of meristic variability since larval specimens were collected (Fig. 66) near the type location of *Ec. anchipterus* and have fewer D_{30} counts (Table 5). Furthermore, although adult distribution is disjunct, the data (Fig. 66) suggest that the "*coheni/anchipterus*" larval form is widely distributed. Little information is available on the occurrence of *Echiodon* larvae in the Indian Ocean (Figs. 66, 67) and we cannot discount the possibility that the observed gaps in distribution are artifactual. Unfortunately, larval data do not resolve the differences in pectoral-fin ray counts (15, 18, 18) among the three available adult specimens since pectoral rays are undeveloped or damaged in our larval material. We note, however, that intra-specific differences between upper and lower limits in adult *Echiodon* pectoral-fin ray counts (Table 4) vary from 1 (in *Ec. exsilium*) to 4 rays (in *Ec. dawsoni*), ranges that encompass the differences considered as diagnostic by Williams (1984a). We stress the need for additional material (see Species Problems section) and consider these forms conspecific.

Echiodon exsilium Rosenblatt
Figure 68

Echiodon exsilium Rosenblatt, 1961: 207, fig. 1 (Gulf of California).

Material Examined: Adults.—SIO 65–292, 10.0–16.9 mm HL, 10 adults of which two are cleared and stained, Mexico, Baja California Sur.

Material Examined: Larvae.—Seven eastern Pacific specimens.

Description: Adult.—Means and ranges of morphometrics of five specimens (10.3–16.5 mm HL, 85–126 mm TL) are as follows, all values reported as a ratio to

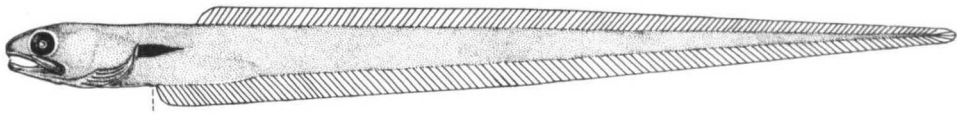


Figure 68. *Echiodon exsiliium*, SIO 65-292, 13.7 mm HL.

HL: SNL 0.19, 0.19–0.20; ED 0.18, 0.17–0.19; UJL 0.48, 0.44–0.50; LJL 0.49, 0.46–0.53; PDL 1.51, 1.44–1.59; PAL 1.23, 1.17–1.26; STA 1.18, 1.10–1.22; PL 0.47, 0.35–0.61; HW 0.29, 0.26–0.33; HD 0.41, 0.38–0.43; BD 0.43, 0.40–0.46; BI 0.13, 0.11–0.15; LTP 1.03, 1.00–1.07. Ranges of meristic values are presented in Table 4. The general appearance of *Ec. exsiliium* is depicted in Figure 68 (also see Rosenblatt, 1961 for a complete description and figure of the holotype). Color in preservative is tan. External melanophores are scattered at the nape of the neck, on the cranium and in a bar pattern below the eye and above the maxilla. Additionally, some pigment is visible on the premaxilla, dentary and behind the eye. Internally, melanophores are scattered over the brain and visible within the snout. The esophagus and anterior stomach are jet black while remaining viscera are unpigmented.

A large, curved fang at the premaxillary tip is separated by a space from small, uniform, conical teeth that are polyserial. The dentary bears 1–2 large fangs followed by a somewhat larger diastema and uniformly small, polyserial, conical teeth. Vomerine teeth are numerous, small, uniform, blunt and conical. Palatine teeth are small, conical and polyserial.

Epipleural ribs on thoracic vertebrae 1–2 are broad, movable and attached distally to the anterior swimbladder wall by ligaments. Parapophyses of vertebrae 3 and 4 are slender, recurved and adhere to the lateral wall of the swimbladder. Subsequent parapophyses of thoracic vertebrae are unmodified. The swimbladder occupies 80–90% of the body cavity, its posterior tip under vertebra 20 in a cleared and stained specimen (SIO 65-292).

Description: Larvae.—Means and ranges of selected morphometric variables for seven specimens (1.3–7.3 mm HL, 12–129 mm TL) are as follows, values reported as a ratio to HL: SNL 0.22, 0.21–0.24; ED 0.25, 0.21–0.31; UJL 0.48, 0.47–0.49; LJL 0.56, 0.47–0.80; PVL 1.71, 1.55–1.88; PDL 1.80, 1.64–2.02; PAL 1.28, 1.18–1.50; STA 1.25, 1.12–1.40; HD 0.64, 0.49–0.92; BD 0.33, 0.26–0.38. Meristic values of two cleared and stained larvae (4.8 and 5.9 mm HL, SWFC uncata.) are: P_1 21–25, A_{30} 50–51, D_{30} 39–42, VVO 9–10, VDO 10–11, VAO 6–7, ARDO 9–11. As noted by Olney and Markle (1979), pectoral-fin ray counts of larval *Ec. exsiliium* generally exceed those of adults, and 1–4 larval rays may be resorbed at metamorphosis (see Characters and Polarity section).

The general appearance of larvae of *Ec. exsiliium* is similar to *Echiodon* unnamed (Fig. 63) and *Ec. dawsoni* (Olney and Markle, 1979). External pigment is limited to a few small melanophores scattered over the cranium. Internally, melanophores are visible on the ventral surface of the hindbrain and on the peritoneum in the dorso-posterior portion of the abdominal cavity. A compensatory tenuis stage is present (Fig. 69).

Premaxillary and dentary dentition in larvae above 4.4 mm HL closely resembles the adult pattern with 1–2 large fangs visible at the jaw tip. In our material, larvae smaller than 3.4 mm HL are toothless.

In a single cleared and stained specimen (4.8 mm HL) epipleural ribs and parapophyses are developed on thoracic vertebrae 1–3 and are identical to those

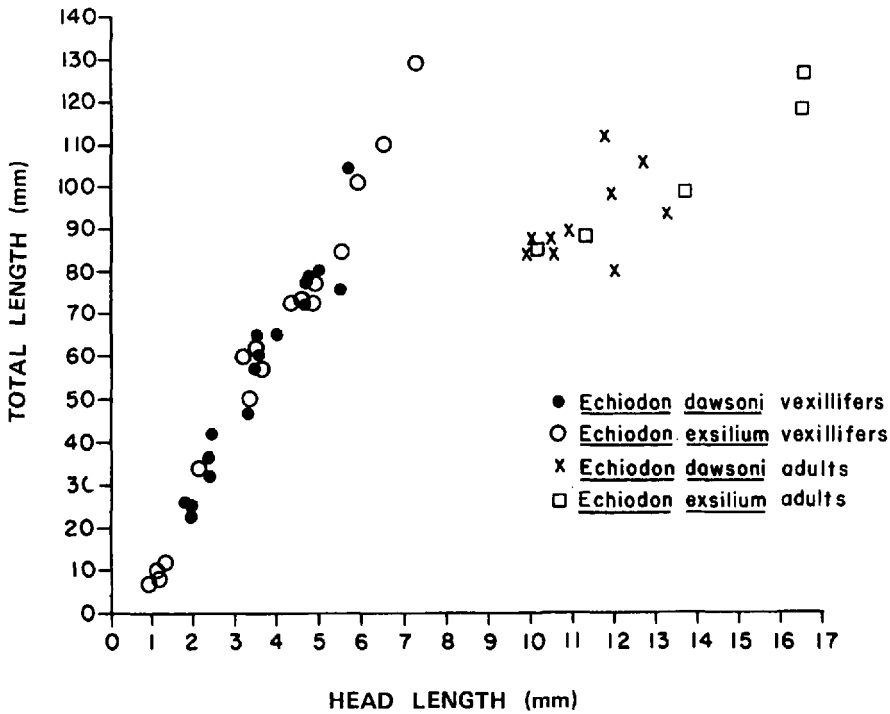


Figure 69. Total length versus head length relationship in *Echiodon dawsoni* and *Ec. exsiliium*.

described for *Ec. dawsoni* (Olney and Markle, 1979). Vertebral centra appear ossified, and neural spines are developing on thoracic vertebrae 1–8. Haemal spines are not visible. All fin rays and supporting elements are fully differentiated. The proximal radial supporting the vexillum is cartilaginous and identical in morphology to that described for *Ec. dawsoni* (Olney and Markle, 1979).

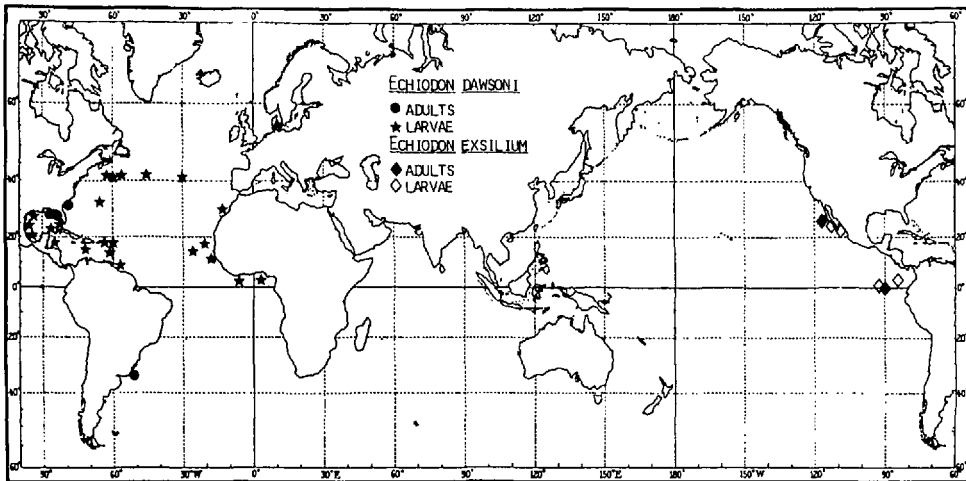


Figure 70. Distribution chart of *Echiodon dawsoni* and *Ec. exsiliium*.

Diagnosis: Adult.—An eastern Pacific (Gulf of California to the Galapagos, Fig. 70) species of *Echiodon* with A_{30} 47–50 and D_{30} 38–42.

Diagnosis: Larvae.—Eastern Pacific *Echiodon* larvae possessing a compound radial supporting the vexillum and first dorsal ray, a posteriorly inserted vexillum (VVO 9–10), A_{30} 50–51 and D_{30} 39–42.

Comments.—The larval morphology of *Ec. dawsoni*, *Ec. exsilium* and *Echiodon* unnamed species is distinctive and suggests close affinity between these three forms.

Echiodon dawsoni Williams and Shipp

Figures 4, 11, 13, 22, 39

Echiodon dawsoni Williams and Shipp, 1982: 846, fig. 2 (Gulf of Mexico).

Echiodon sp. A: Williams and Shipp, 1982: 851 (off Brazil).

Echiodon sp.: Olney and Markle, 1979: 367, figs. 1, 3–5 (larvae).

Type Material Examined.—*Echiodon dawsoni*, PARATYPE, UF 30886, 10.3 mm HL, cleared and stained, Gulf of Mexico, 29°39'50"N, 87°16'12"W, 75.6 m, 7 Feb 1978, collected with holotype; *Ec. dawsoni*, PARATYPE, USA 6006, two juvenile (5.4, 6.5 mm HL) and four larval specimens (3.2–3.9 mm HL), same collection data as above; *Ec. dawsoni*, PARATYPE, USA 6008, one adult (8.9 mm HL) and two larvae (3.3–4.0 mm HL), 29°30'N, 86°25'W, 155–173 m. [References by Williams and Shipp, 1982 to *tenuis* larvae may include damaged vexillifers. Our HL/TL plot (Fig. 69) failed to show any individuals in the compensatory shrinking phase. Rather, all nominal "*tenuis*" individuals fell on the larval growth curve.]

Other Material Examined: Adult.—8 lots; off eastern United States and southern Brazil.

Other Material Examined: Larvae.—63 lots; various Atlantic localities.

Description: Adult.—Morphometrics of available specimens are presented in Table 11. Meristic ranges of six western Atlantic and three Brazilian specimens (MZUSP 9988) are as follows, those of Brazilian material in parentheses: P_1 17–20 (18–21), A_{30} 39–43 (40), D_{30} 28–35 (30), VDO 11–12 (13), VAO 6(7), PCV 21–25 (21–23), ARDO 11–12 (12). Descriptions and illustrations of *Ec. dawsoni* are presented by Williams and Shipp (1982). Color in preservative cream to tan. Pigment in the form of large, stellate melanophores is primarily internal and distributed over the entire brain, around the ventral margin of the eye, the snout, lower jaw and vertebrae. Vertebral pigment is conspicuous posteriorly becoming less visible anteriorly due to epaxial musculature. Stomach color is geographically variable in our material. Available specimens from western Atlantic localities lack pigment while in three specimens from off Brazil the esophagus and anterior stomach are black.

The premaxilla and dentary bear 1–2 large, curved fangs separated by a space from small, polyserial, conical teeth, those of the dentary somewhat larger. Palatine teeth are small, conical and polyserial; vomerine teeth are small, uniform, blunt and conical.

Epipleural ribs and parapophyses on thoracic vertebrae are identical to those described for *Ec. exsilium*. The swimbladder occupies 70–90% of the body cavity, its posterior tip under vertebrae 16–20 in two cleared and stained specimens.

Description: Larvae.—Means, ranges and standard deviation of selected morphometrics (expressed as a ratio to the HL) in a sample of 20 specimens (0.5–3.9 mm HL) are as follows: SNL 0.26, 0.20–0.32, 0.03; UJL 0.47, 0.37–0.58, 0.05; LJL 0.68, 0.54–0.89, 0.09; PVO 1.99, 1.77–2.28, 0.13; PDL 2.08, 1.91–2.40, 0.16; PAL 1.35, 1.20–1.50, 0.09; STA 1.34, 1.19–1.66, 0.12. Meristic ranges of two cleared and stained western Atlantic vexillifers (3.7–3.9 mm HL) are as follows:

Table 11. Comparison of selected measurements in adults of two populations of *Echiodon dawsoni* (All values except HL and TL expressed as a ratio to HL)

	Western Atlantic			Off Brazil		
	N	\bar{x}	Range	N	\bar{x}	Range
HL (mm)	3	—	10.0–12.7	3	—	10.4–13.3
TL (mm)	3	—	84–112	3	—	80–94
SNL	3	0.2	0.1–0.19	3	0.2	0.2–0.2
ED	3	0.2	0.2–0.19	3	0.2	0.2–0.2
UJL	3	0.5	0.5–0.52	3	0.6	0.5–0.6
LJL	3	0.5	0.5–0.51	3	0.5	0.5–0.6
PDL	3	1.8	1.8–1.9	1	—	1.7
PAL	3	1.2	1.1–1.3	2	1.2	1.1–1.2
HW	3	0.3	0.3–0.34	3	0.3	0.3–0.3
HD	3	0.4	0.4–0.42	3	0.5	0.4–0.5
BI	3	0.1	0.1–0.14	3	0.2	0.1–0.2

P₁ 18, A₃₀ 38, D₃₀ 29–30, VVO 11, VDO 11–12, VAO 6, ARDO 10–11. A detailed description of vexillifers of *Ec. dawsoni* is presented by Olney and Markle (1979). External pigment is limited to a few small melanophores scattered over the cranium. Internally, melanophores are scattered on the ventral hindbrain and on the peritoneum in the dorso-posterior portion of the abdominal cavity.

Comments.—The three South Atlantic specimens have a black esophagus and anterior stomach, slightly higher VDO and VAO values and slightly larger jaw length and head depth (Table 11) when compared to western Atlantic material. We did not observe differences in precaudal vertebrae or interorbital width as reported by Williams and Shipp (1982). No additional material from the South Atlantic is available and, although the present data may suggest two allopatric species, we have no more information on morphological variability than was available to Williams and Shipp (1982) or Williams (1984a). As a result, we follow these authors in considering the Brazilian population in an unresolved taxonomic status and conspecific with *Ec. dawsoni*.

Echiodon neotes new species

Figure 71

Type Material Examined.—*Echiodon neotes*, HOLOTYPE, ZMUC, 13.0 mm HL, 157 mm TL, female ?, 35°16'S, 178°40'W, Kermadec Trench, 82–8,300 m, GALATHEA Expedition, 14 II 1952, ST600/11.700.

Description of Type Material.—Morphometrics expressed as a ratio to HL are as follows, actual measurements (mm) in parentheses: SNL 0.25 (3.3), ED 0.16 (2.1), UJL 0.52 (6.7), LJL 0.48 (6.3), VL 1.13 (14.7), PVL 1.25 (16.3), PDL 1.27 (16.5), PAL 1.29 (16.8), STA 1.25 (16.3), PL ca. 0.31 (ca. 4), HW 0.30 (3.5), HD 0.46 (6.0), BD 0.48 (6.2), BI 0.12 (1.5). Meristics are presented in Table 4. It should be noted that the value of D₃₀ is based on myomere examination since dorsal rays were not visible in a radiograph. The general appearance of *Ec. neotes* is depicted in Figure 71. The holotype (an only known specimen) is tan in alcohol. Faded, stellate melanophores are scattered over the fore- and midbrain and the iris is black, otherwise, the body is unpigmented.

Each premaxilla bears a single, large fang that is somewhat curved and protrudes down from the upper lip to the midpoint of the tip of the lower jaw (the mouth



Figure 71. *Echiodon neotes*, holotype, ZMUC Galathea, 13.0 mm HL.

is closed). Small, curved, conical teeth are separated from the anterior fang by a space and are polyserial. Dentary dentition is similar to that of the premaxilla except each dentary bears 1–2 large fangs that are approximately twice the size of the premaxillary fangs. The vomer bears a single stout, conical tooth that is

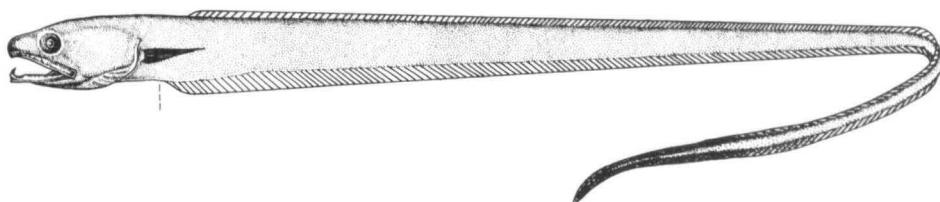


Figure 72. *Echiodon drummondi*, DAFS uncat., 24 mm HL.

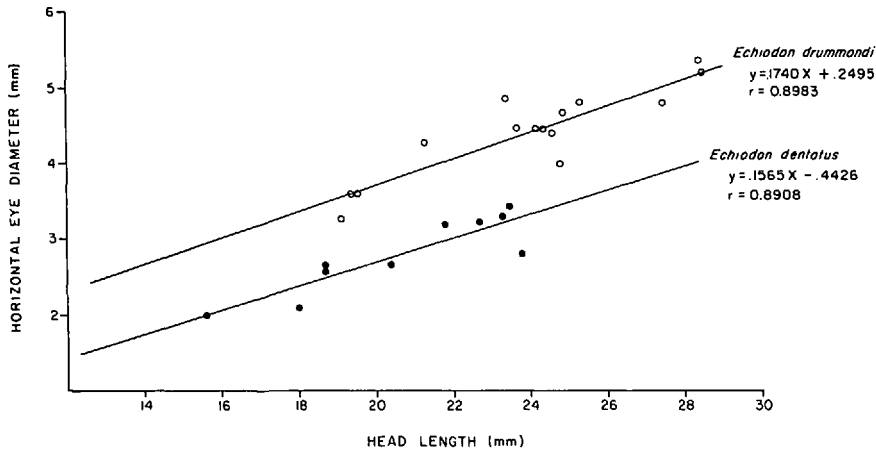


Figure 73. Regression of horizontal eye diameter versus head length in adult *Echiodon drummondi* and *Ec. dentatus*.

medial, blunt and surrounded by smaller, conical, blunt teeth. Palatine teeth are conical and polyserial, those of the inner rows somewhat larger.

The holotype has a vexillum that inserts above and slightly anterior to a vertical through the anus. The first dorsal ray is inserted directly above the first anal ray. The pectoral-fin base is anterior to the vexillar insertion and vent. A caudal fin is absent.

Description: Larvae.—The holotype may be a larva (see Comments).

Diagnosis: Adult.—A species of *Echiodon* with 35 precaudal vertebrae, 19–20 pectoral rays and A_{30} 47. The species may be deep-dwelling and neotenic in the retention of a vexillum as an adult (see Comments).

Comments.—We have had difficulty classifying this unusual specimen. The possession of a vexillum, pelagic capture and our inability to confidently determine sex suggest the holotype may be a larva. Alternatively, considering the free-living habit and frequent pelagic capture of its congeners, the large size of the holotype

Table 12. Comparison of selected morphometrics in North Sea (*Echiodon drummondi*) and Mediterranean (*E. dentatus*) populations of *Echiodon* (All values except HL and TL expressed as a ratio to HL)

	<i>Ec. drummondi</i>				<i>Ec. dentatus</i>			
	N	\bar{x}	Range	SD	N	\bar{x}	Range	SD
HL (mm)	12	—	19.1–28.4	—	10	—	9.9–23.8	—
TL (mm)	12	—	163–267	—	10	—	75–235	—
SNL	12	0.2	0.2–0.2	0.02	10	0.2	0.2–0.3	0.03
ED	26	0.2	0.2–0.2	0.01	14	0.1	0.1–0.2	0.02
UJL	12	0.5	0.5–0.5	0.02	10	0.5	0.5–0.5	0.02
LJL	12	0.5	0.5–0.5	0.02	10	0.5	0.5–0.6	0.02
PDL	8	1.4	1.3–1.5	0.05	9	1.4	1.4–1.5	0.07
PAL	12	1.3	1.2–1.4	0.05	10	1.2	1.1–1.3	0.08
STA	3	1.2	1.2–1.2	0.01	9	1.2	1.1–1.3	0.08
PL	12	0.5	0.4–0.6	0.04	7	0.5	0.5–0.6	0.05
HD	12	0.4	0.4–0.5	0.03	10	0.4	0.4–0.5	0.02
BD	12	0.5	0.4–0.5	0.03	10	0.4	0.4–0.4	0.03

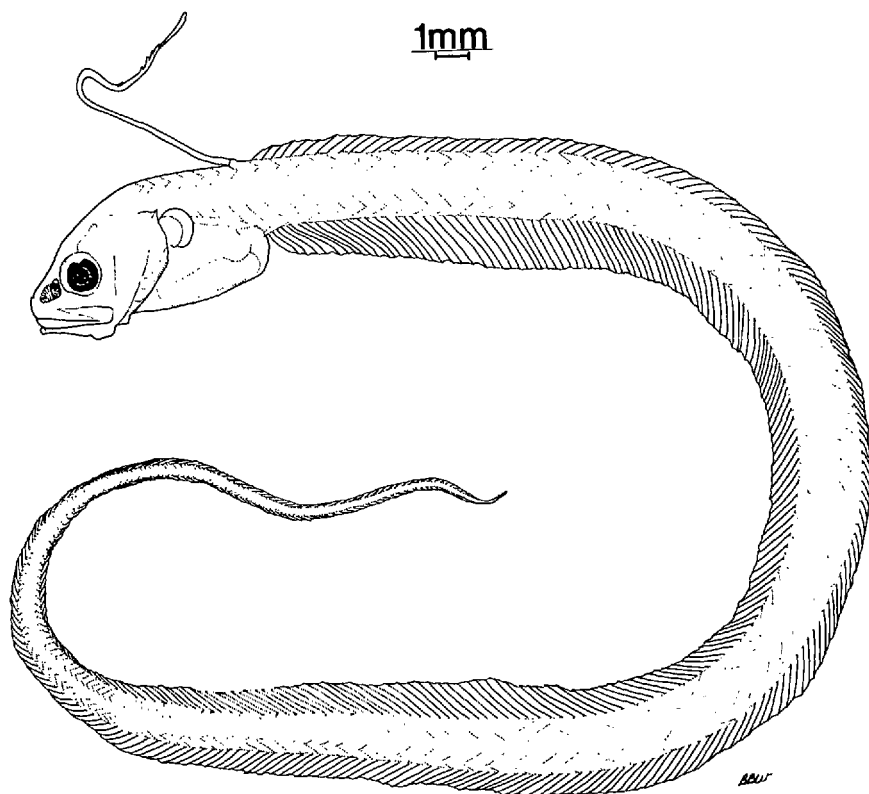


Figure 74. *Echiodon drummondi*, ZMUC DANA 8371, 3.8 mm HL. Reproduced with permission from Gordon et al. (1984).

as well as the difficulty in determining sex in some non-gravid carapid specimens, the holotype may represent the first capture of a neotenic adult pearlfish. Regardless of these opposing choices of life history designation (i.e., larva or adult) the holotype is not referable to any known species of *Echiodon* based on morphological and meristic criteria. *Echiodon neotes* shares a high precaudal vertebral count with *Ec. rendahli* but has a greater number of pectoral-fin rays and a higher A_{30} value. Additionally, larvae of *Ec. rendahli* are described, and the holotype of *Ec. neotes* does not fit the observed growth patterns in either *Ec. rendahli* or the apparently allopatric *Eurypleuron owasianum* (Fig. 57, see comments in the *Echiodon rendahli* species account).

Etymology. — The species name is derived from the Greek “neotes” meaning youth and refers to the presence of larval characteristics in the holotype. The name should be treated as a noun in apposition.

Echiodon drummondi Thompson
Figures 4, 11, 13, 20, 72, 74

Echiodon drummondii Thompson, 1837: 55 (coast of County Antrim, Northern Ireland).

Neotype Designation. — Arnold (1956) was unable to locate Thompson's (1837) type and the single specimen (approximately 280 mm TL, collected on the coast of Antrim County, Northern Ireland) was not listed in the collections of BMNH or MNHN-Paris (Wheeler, pers. comm., 24 March 1982; Bauchot, pers. comm.), the NMI (O'Riordon, pers. comm., 25 Nov. 1987) or the Ulster Museum,

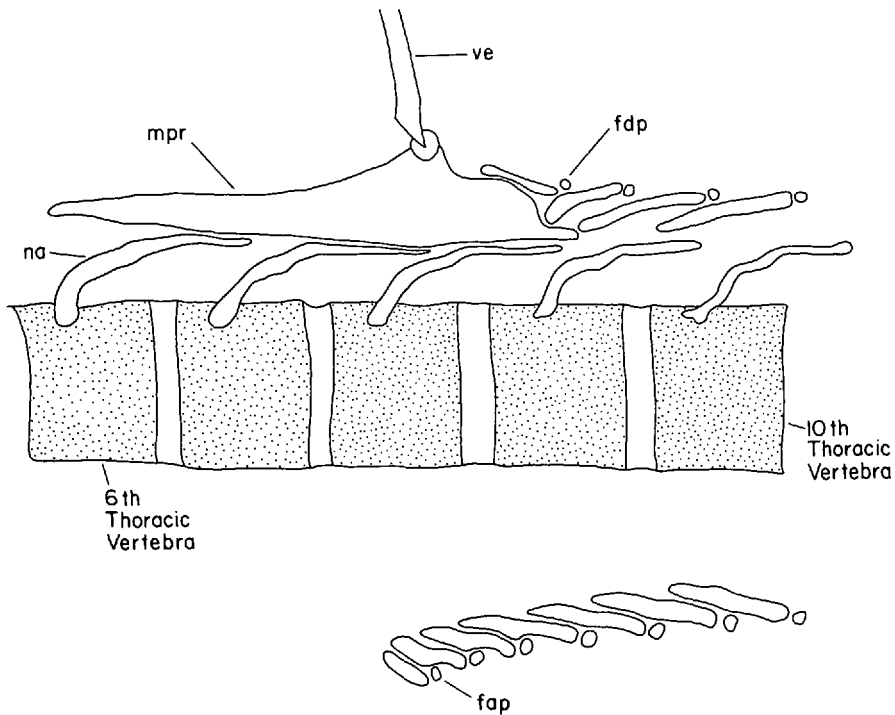


Figure 75. Vexillar supporting radial and associated structure in larval *Echiodon drummondi*, DAFS uncat., 4.6 mm HL.

Belfast (Erwin, pers. comm., 17 Dec. 1987). Although the OUM possesses crustacean material collected by Thompson, there are no fish and the holotype is considered lost (Hull, pers. comm., 3 Feb. 1988). Since there is the potential for further taxonomic confusion with *Ec. dentatus*, we designate the following neotype.

Type Material Examined.—*Echiodon drummondi*: NEOTYPE, ZMUC DANA St. 10674, a male 24.6 mm HL, 238 MM TL, 60°00'N, 3°00'E, DANA St. 10674, 28 September 1957.

Other Material Examined: Adult.—18 lots; North Sea and eastern Atlantic localities.

Other Material Examined: Larvae.—105 lots; central and eastern Atlantic localities.

Description: Adult.—Adults of *Ec. drummondi* are delimited from those of *Ec. dentatus* on the basis of morphometry (Fig. 73) and distribution. In the material at hand ($N = 40$) the eye diameters of only seven specimens (14–19% of each sample; *Ec. drummondi* 5 of 26, *Ec. dentatus* 2 of 14) fell into the range of overlapping values (0.16–0.17 ED/HL). Morphometric variables are summarized in Table 12 and meristic ranges are presented in Table 4. The general appearance of *Ec. drummondi* is depicted in Figure 72. Color in preservative is tan to brown. Externally, small melanophores are visible at the tip of the snout and lower jaw and along the anterior half of the upper jaw. Melanophores are scattered over the cranium and nape of the neck. Larger, stellate melanophores are densely scattered on the posterior tenth of the caudal portion where dorsal and anal fin rays are darkly pigmented. Melanophores become subdermal anteriorly and are visible in association with the vertebral column and dorsal- and anal-fin pterygiophores. Stellate melanophores are scattered on the peritoneum. The swimbladder is largely unpigmented. The esophagus and anterior stomach are black.

The swimbladder bears a posterior, intrinsic constriction in males, a condition that is identical to that in males of *Ec. dentatus* (Fig. 35).

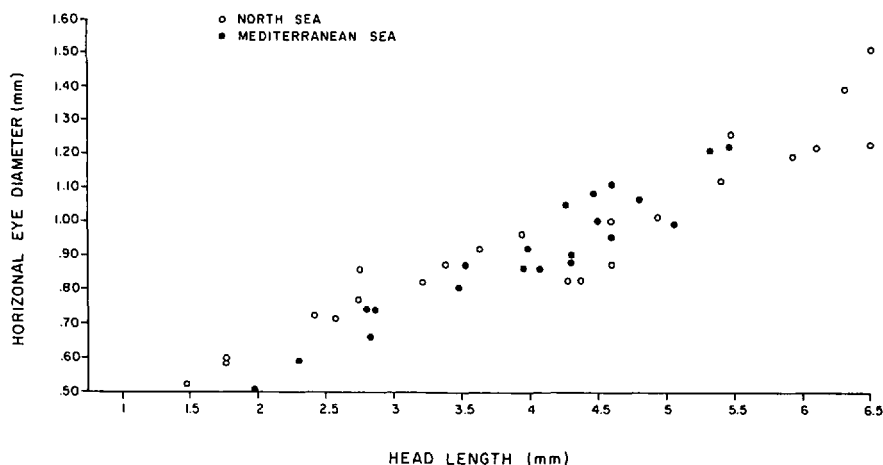


Figure 76. Horizontal eye diameter versus head length in North Sea and Mediterranean vexillifers of *Echiodon* spp.

Description: Larvae.—Ranges of selected morphometrics in four North Sea specimens (4.6–6.5 mm HL, 72–93 mm TL) are as follows, values expressed as a ratio to HL: SNL 0.26–0.33, ED 0.18–0.22, UJL 0.43–0.52, LJL 0.54–0.59, VL 2.19–3.37, PVL 1.51–1.74, PDL 1.63–1.83, PAL 1.42–1.65, STA 1.39–1.63, HW 0.34–0.36, HD 0.61–0.80, BD 0.40–0.49, BI 0.17–0.18. Larval meristics are presented in Table 5. The vexillifer larva of *Ec. drummondi* is illustrated in Figures 74 and 75. Comparisons of horizontal eye diameter relative to HL in 23 North Sea specimens and 21 Mediterranean vexillifers (Fig. 76) did not allow delimitation of larvae of *Ec. drummondi* and *Ec. dentatus*. As a result, our identification of larvae of these closely related species is based solely on distribution. The HL/TL relationship is illustrated in Figure 77.

Diagnosis: Adult.—A species of *Echiodon* of the northeastern Atlantic and North Sea with ARDO 2–7, PCV 26–29 and a large eye (ED/HL ranging from 0.16–0.21, \bar{x} 0.19).

Diagnosis: Larvae.—*Echiodon* larvae of the northeast Atlantic and North Sea with a simple proximal radial supporting the vexillum, VVO 7–8, A_{30} 48, D_{30} 43, ARDO 4–5 and a pouchlike gut.

Comments.—The sexually dimorphic swimbladder of *E. drummondi* and *E. dentatus* may be unique in the genus although there is some evidence of a similar condition in *E. rendahli* (see below). In contrast with the observations of Williams and Shipp (1982), we found the presence of lateral line pores to be variable among specimens in these two taxa.

Adults of *E. drummondi* may aggregate in large spawning assemblages. Collections of the R/V DANA and of the Fisheries Research Board of Scotland have yielded large numbers of running ripe adults in single trawl hauls.

Echiodon dentatus (Cuvier)

Figure 35

Ophidium dentatus Cuvier, 1829: 239 (Mediterranean).

Carapus imberbis: Aboussouan, 1972: 174, fig. 7 (off West Africa).

Type Material Examined.—Arnold (1956: 292) was convinced that Cuvier's types were lost. We

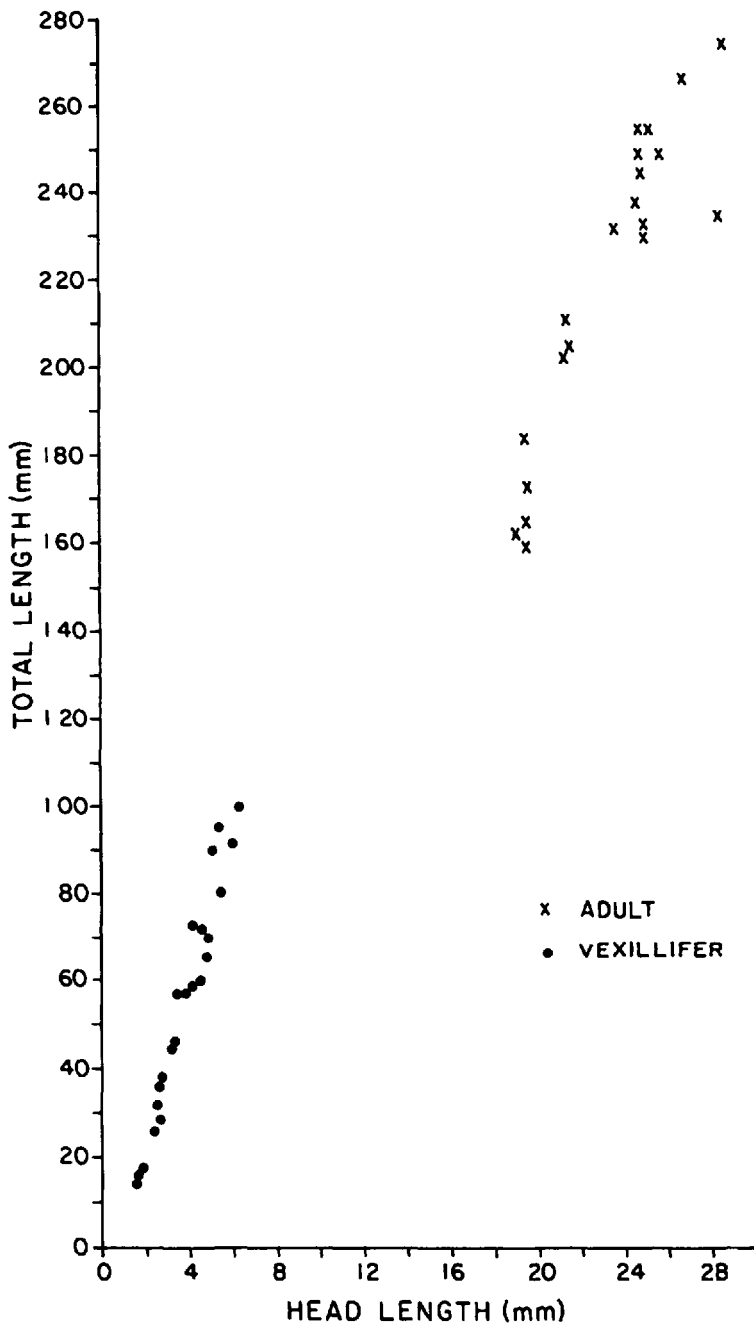


Figure 77. Total length versus head length relationship in *Ec. drummondii*.

examined a radiograph of nine adults (some with damaged fins) bearing the label "MNHN-Paris B1268, *Fierasfer dentatus* TYPES."

Other Material Examined: Adult.—11 lots; Mediterranean and eastern Atlantic localities.

Other Material Examined: Larvae.—36 lots; Mediterranean localities.

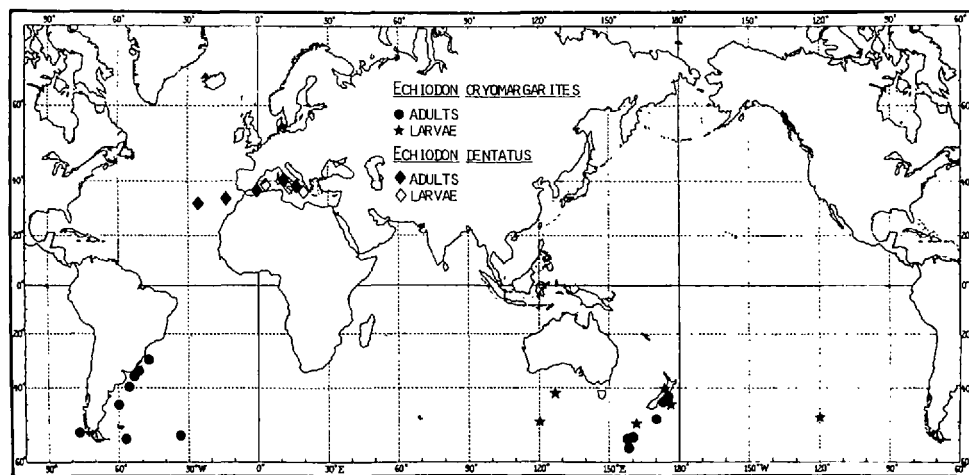


Figure 78. Distribution chart of *Echiodon cryomargarites* and *Ec. dentatus*.

Description: Adult.—Morphometric variables are summarized in Table 12 and meristic data are presented in Table 4. Adults of *Ec. dentatus* are similar in appearance to adults of *Ec. drummondi* (Fig. 72) but can be distinguished on the basis of eye diameter (Fig. 73). The reader is referred to the preceding section for a general description of *Ec. drummondi/dentatus* morphology and pigmentation.

Description: Larvae.—Meristics of larval *Ec. dentatus* collected in Mediterranean localities are presented in Table 5. Larvae of *Ec. dentatus* are similar in general appearance to those of *Ec. drummondi* (Fig. 74) and cannot be delimited on the basis of eye diameter (Fig. 76).

Comments.—Aboussouan (1972) illustrates and briefly describes a 1.5 mm HL pearlfish larva collected off West Africa. We have not examined the specimen but believe it to be referable to *Ec. dentatus* on the basis of vexillum position and distribution (Fig. 78).

Echiodon pegasus new species Figure 79

Type Material Examined.—*Echiodon pegasus*, HOLOTYPE, NMNZ P16529, 24.3 mm HL, 200 mm TL, male, Auckland I. shelf, New Zealand, 26 Mar 1979, R/V WESERMUNDE W.2/7/79. *Echiodon pegasus*, PARATYPES, NMNZ P14550, 13.8 mm HL, 120 mm TL, female, 43°22'S, 173°44'E, Pegasus Bight, 117 m, 25 July 1983, R/V KALTAN; NMNZ P16528, 13.7 mm HL, ca. 118 mm TL (twisted), 43°59.8'–56.8'S, 173°49.1'–56.1'E, off Banks Peninsula, 228–239 m, 8 Nov 1976, R/V W.J. SCOTT; NMNZ P20999, 13.0 mm HL, 124 mm TL, 43°32.0'–30.0'S, 176°03.0'–11.0'W, east of Chatham Is., 230–210 m, 24 May 1987, R/V OYANG 7.

Description of Type Material.—Morphometric variables expressed as a ratio to HL of the holotype are as follows, upper and lower ranges of the paratypes in parentheses: SNL 0.20 (0.21), ED 0.18 (0.20–0.23), UJL 0.48 (0.53–0.54), LJL 0.47 (0.49–0.53), PDL 1.55 (1.52–1.81), PAL 1.25 (1.19–1.48), STA 1.19 (1.09), PL 0.50 (0.55–0.69), HW 0.34 (0.35–0.36), HD 0.44 (0.36–0.54), BD 0.46 (0.43–0.59), BI 0.15 (0.16–0.19). Ranges of meristic variables of *Ec. pegasus* are reported in Table 4, those of the holotype as follows: P₁ 15, 16, A₃₀ 45, D₃₀ 38, PCV 29, VDO 11, VAO 8, ARDO 6. The general appearance of the holotype is shown in Figure 79. Color in alcohol is tan. Stellate melanophores are concentrated on the



Figure 79. *Echiodon pegasus*, holotype, NMNZ P.16529, 24.3 mm HL.

cranium and nape of the neck. A single row of melanophores is visible along either side of the dorsal fin extending to the tip of the tail. In addition, melanophores at the base of each dorsal ray form a mid-dorsal row extending to the tail tip. This dorsal pigment pattern is absent in the smaller paratype. Stellate melanophores are scattered at the tail tip where both dorsal and anal fin rays are darkly pigmented. The caudal fin, visible on the holotype, is unpigmented. Me-

lanophores are associated with fin ray bases on the posterior half of the anal fin. Some pigment associated with vertebral centra is visible at the tail tip. The esophagus, stomach and intestines are black, and melanophores are scattered on the peritoneum and swimbladder. The gill arches are darkly pigmented and the tongue is darkly pigmented in the holotype. Melanophores are scattered on the snout, jaw tips and in a ventral series partially encircling the eye.

The fleshy snout and upper lip partially obscure two fangs at the symphysis of the premaxillae. The inner-most fang is smaller, depressible and separated by a space from a band of small conical teeth that are polyserial, inwardly curved and extend to the posterior tip. Dentary dentition is similar to that described above (the left pair of fangs is damaged in the holotype). The vomer bears a median patch of irregularly spaced, blunt, short, conical teeth surrounded by smaller teeth of similar shape. Palatine teeth are short, conical and polyserial.

The swimbladder occupies the anterior half of the body cavity and possesses a left ventro-lateral patch of tunic ridges. In the holotype (male) the tunic is thick, and the swimbladder is uniform in size and shape with no intrinsic constrictions. In the female paratype the posterior portion of the swimbladder is expanded, but no intrinsic constriction is visible.

The testes are conspicuously bilobate with the longest lobe (ca. 6 mm) extending to the swimbladder terminus.

One paratype (NMNZ P20999) is parasitized by several copepods attached behind the head and behind the anus.

Description: Larva.—The larva of *Ec. pegasus* is unknown.

Diagnosis: Adult.—A species of *Echiodon* with 14–16 pectoral-fin rays, PCV 28–29, ARDO 6 and VDO 11–12.

Comments.—*Echiodon pegasus* can be delimited from its sympatric congeners, *Ec. cryomargarites* and *Ec. pukaki*, on the basis of pectoral-fin rays (14–16 vs. 19–26), ARDO values (6 vs. 9–12) and gross morphology (relatively short, stubby body attaining 200 mm TL in adult males vs. long, attenuate body attaining 410 mm TL and 232 mm TL, respectively). The apparently allopatric *Ec. rendahli* differs from *Ec. pegasus* in that it possesses more than 30 precaudal vertebrae (Table 4).

Echiodon cryomargarites Markle, Williams and Olney
Figures 22, 29, 39, 80, 81

Echiodon cryomargarites Markle, Williams and Olney, 1983: 647, fig. 1 (Southern Ocean).

Echiodon specimens: Markle, Williams and Olney, 1983: 654, fig. 1 (off Chile).

Type Material Examined.—*Echiodon cryomargarites*, Holotype, LACM 10985-6, 37.3 mm HL, 419 mm TL, male, ELTANIN Station 1422, 56°19'–21'S, 158°29'E, 12 Feb 1965, 3 m Blake trawl, 833–842 m bottom depth range. *Echiodon cryomargarites*, Paratypes, LACM 10985-8, 3 specimens, 21.8–27.3 mm HL, 230–310 mm TL, males, caught with holotype. Additional paratype material examined is listed by Markle et al. (1983).

Other Adult Material Examined.—16 lots, Argentina, Brazil, New Zealand localities.

Larval Material Examined.—9 lots, Antarctic and adjacent seas.

Description: Adult.—The general appearance of *Echiodon cryomargarites* is depicted in Figure 80 and full adult descriptions as well as additional illustrations are presented by Markle et al. (1983). In the holotype, the tunic is thick and distinct tunic ridges are located left laterally on the posterior swimbladder. This condition was not noted by Markle et al. (1983). "Intrinsic" swimbladder con-

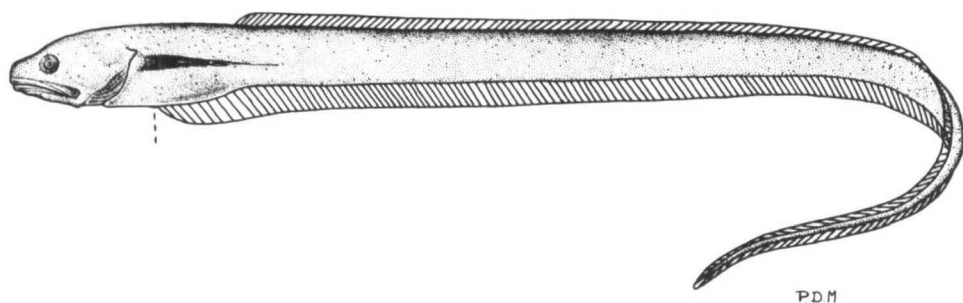


Figure 80. *Echiodon cryomargarites*, LACM 42593-001, 30.8 mm HL.

strictions are absent in the material examined and swimbladder morphology is not sexually dimorphic. We now believe the Chilean specimens, previously referred to an uncertain form (Markle et al., 1983), are simply a regional variant (Zama and Cardenas, 1984).

Description: Larvae.—The general appearance of larval *Ec. cryomargarites* is depicted in Figure 81 and descriptions of larvae (including additional illustrations) are presented by Markle et al. (1983). Larvae were originally identified by Markle et al. (1983) on the basis of distributional data and unique meristic characters (primarily PCV and D_{30}); however, we now note the potential for confusion of this material with larvae (presently unknown) of sympatric *Ec. pukaki* and *Ec. pegasus* (Figs. 67, 78). Larval *Ec. cryomargarites* can be distinguished from larvae of sympatric *Ec. coheni* and *Ec. rendahli* on the basis of PCV, D_{30} and A_{30} counts (Table 5). Larvae of *Ec. pegasus* and *Ec. pukaki* are unknown, and available meristic data (Tables 4, 5) indicate that A_{30} counts of larval *Ec. cryomargarites* overlap those of *Ec. pegasus*. In our larval material, D_{30} counts are higher than those of adults of either *Ec. pegasus* or *Ec. pukaki*, and it is on this admittedly uncertain basis that we retain the Markle et al. (1983) allocation of this material. These identifications must be considered tentative, however, until additional adult and larval material of these three southern ocean *Echiodon* species are available.

Diagnosis: Adult.—A southern ocean species of *Echiodon* with P_1 19–21, PCV 25–29 and ARDO 9–12.

Diagnosis: Larvae.—A southern ocean *Echiodon* larva possessing a sac-like protruding gut, ARDO 6–7 and PCV 26–28 (but see preceding section).

Comments.—Our additional adult and larval material (Fig. 78) does not appreciably alter the distributional data presented by Markle et al. (1983). The species was recently collected by Stehman (pers. comm.) from 53°56'S, 35°40'W, the eastern slope off South Georgia Island, at a depth of 800 m.

Echiodon rendahli (Whitley)

Figure 82

Carapus rendahli Whitley, 1941: 40, fig. 27 (Port Jackson, New South Wales, Australia).

Type Material Examined.—*Carapus rendahli*, HOLOTYPE, AMS I.2411, 11.0 mm HL, 93 mm TL (both measurements after Whitley, 1941), gravid female, Port Jackson, New South Wales, Jan. 1889, purchased.

Other Material Examined: Adult.—6 lots; southern Australia and New Zealand.

Other Material Examined: Larvae.—4 lots; southern and eastern Australia.

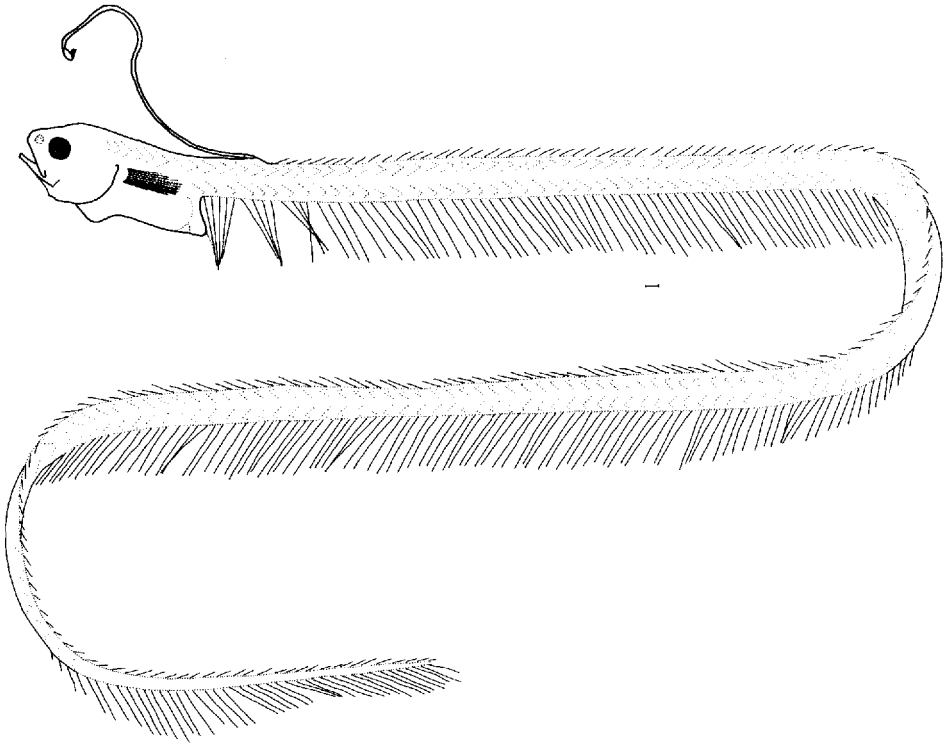


Figure 81. *Echiodon cryomargarites*, LACM 42592-001, 7.9 mm HL.

Description: Adult.—The holotype is badly damaged (broken into two pieces at vertebra 18) and poorly preserved. The following measurements (mm) were obtained from the specimen: SNL 1.9, ED 2.3, UJL 5.6, LJL 6.1. Means and extremes in values of selected morphometric variables in five adults (8.5–15.0 mm HL, 69–141 mm TL) are as follows, values expressed as a ratio to HL: SL 0.19, 0.18–0.20; ED 0.19, 0.18–0.21; UJL 0.51, 0.47–0.58; LJL 0.48, 0.43–0.53; PDL 1.36, 1.18–1.47; PAL 1.23, 1.10–1.40; STA 1.20, 1.04–1.35; PL 0.52, 0.46–0.59; HD 0.44, 0.40–0.54; BD 0.45, 0.40–0.54. The anterior and posterior portions of the broken holotype possess 18 and 27 thoracic vertebrae, respectively (totaling 35 PCV, presuming none were lost or destroyed at the break). We are unable to obtain additional meristic data from the type but note that Williams (1984a) reports A_{30} 38, D_{30} 43, PCV 35, VDO 7–8, VAO 8, VPB 7, P_1 15. Ranges of meristic data of six additional specimens are: P_1 14–17, A_{30} 37–38, D_{30} 40–41, PCV 31–34, VDO 7, VAO 5–7, VPB 6–7, ARDO 0–4. Our material did not include a specimen from Tasmania, Australia (QVM 1977/5/32) examined by Williams (1984a). Table 4 summarizes meristic data in *Ec. rendahli* including those observations of Williams (1984a).

The general appearance of *Ec. rendahli* is depicted in Williams (1984a). Color in preservative pale to brown. Stellate melanophores are scattered over the cranium and a few appear at the nape of the neck. Additional external pigment is limited to a few scattered melanophores on the snout and darkly pigmented dorsal- and anal-fin rays on the posterior tenth of the body. Pigment is associated with dorsal- and anal-fin supports along the posterior third of the body. The abdomen appears dark, a condition resulting from large stellate melanophores densely scat-

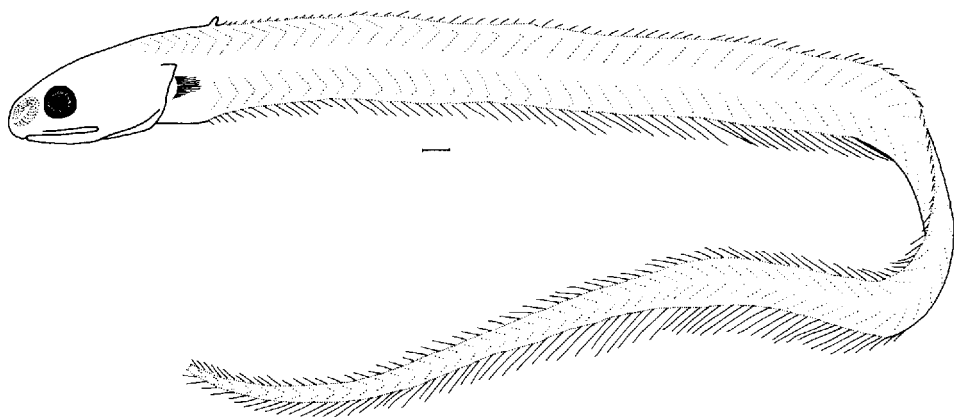


Figure 82. *Echiodon rendahli*, USNM 301666, 5.7 mm HL.

tered on the peritoneum. Williams (1984a) reported a silvery peritoneum in the Tasmanian specimen, but only the swimbladder appears silver (chalky white scattered with stellate melanophores) in our material. The esophagus and stomach are black. Intestine lacks pigment or has scattered melanophores. The gill arches and inner gill cover are darkly pigmented.

The premaxilla bears one or two large, curved canines that protrude down from the upper lip to well below the lower jaw when the mouth is closed. Each dentary bears a single, large fang (two in a Tasmanian specimen examined by Williams, 1984a) that fits into well defined depressions on either side of the ethmoid. In both upper and lower jaws, these fangs are separated by a space from small, conical, polyserial teeth (about three rows on the premaxilla, five on the dentary). Vomer with a patch of irregularly spaced short, blunt conical teeth, those of the median crest somewhat larger. Palatine teeth conical, small, polyserial.

The swimbladder occupies the entire length of the body cavity, bears a ventral patch of tunic ridges, and (in one male specimen) is separated from the anterior swimbladder by an intrinsic constriction. In a second male, the swimbladder is damaged and in all females (the holotype plus AMS IB.7135, AMS IB.4353) this constriction is absent. We conclude that swimbladder morphology varies and may be sexually dimorphic in *Ec. rendahli* (*Ec. drummondi* section, Fig. 35).

Description: Larva.—Means and ranges of selected morphometrics in four specimens (4.5–7.3 mm HL, 45–74 mm TL) are as follows, values expressed as a ratio to HL: SNL 0.23, 0.19–0.25; ED 0.20, 0.18–0.21; UJL 0.45, 0.42–0.46; LJL 0.46, 0.41–0.47; VL 1.16, 0.87–1.44; PVL 1.27, 1.17–1.36; PDL 1.31, 1.19–1.40; PAL 1.20, 1.12–1.34; STA 1.14, 1.09–1.21; PL 0.29, 0.24–0.33; HD 0.44, 0.42–0.46; BD 0.44, 0.38–0.54. Meristic variables are summarized in Table 5. Precaudal vertebral ranges are based on radiographs of two large specimens (ZMUC uncat., 7.3 mm HL; AMS I.16492 6.2 mm HL), and A_{30} , D_{30} values are based on myomere counts (Table 5). The general appearance of the vexillifer larva of *Ec. rendahli* is depicted in Figure 82. The illustrated specimen (USNM 301666, 5.7 mm HL) possesses faded melanophores at the tip of the snout and lower jaw but lacks any additional pigment. In larger specimens, large stellate melanophores are scattered over the cranium and hindbrain and along the posterior tenth of the caudal portion.

Diagnosis: Adult.—A species of *Echiodon* with 14–17 pectoral-fin rays, more than 30 precaudal vertebrae, A_{30} 37–38 and D_{30} 40–43.

Diagnosis: Larva.—An *Echiodon* larva lacking a pouch-like gut and with the vexillum inserted over or slightly posterior to a vertical through the anal-fin origin, ARDO 5–6, A₃₀ 45, D₃₀ 40–41, MVO 7 and distributed along eastern and southern Australia.

Comments.—Whitley (1941) provisionally identified an exterilium larva as belonging to *Ec. rendahli*, an assignment followed by Robertson (1975) and Gordon et al. (1984). Our meristic analysis of adult *Eu. owasianum* and *Ec. rendahli* reveals disparity in precaudal vertebral number (22–25 vs. 31–35, Table 4), and the identification of the larva of *Ec. rendahli* is in part based on these values (Table 5). However, delayed development of vertebral centra in larval *Eu. owasianum* does not permit accurate PCV counts. Thus, we cannot confirm that this character will delimit larvae of these species. Only *Ec. neotes* possesses PCV counts greater than 30. Identification of larval *Ec. rendahli* is further confounded by an inexplicably high A₃₀ count that is not consistent with values from adult *Ec. rendahli* and overlaps that of *Ec. neotes* (Tables 4, 5). We note that this single A₃₀ value for *Ec. rendahli* larvae resulted from myomere examination rather than a preferred radiological or staining method and may be in error. Our resolution of this problem is based on examination of growth plots of available material. The extreme size of the single specimen of *Ec. neotes* places it far outside of the expected HL/TL plot of either *Ec. rendahli* or *Eu. owasianum* (Fig. 57) and supports the notion that this specimen represents a distinct taxon (see the preceding description of *Ec. neotes*). The TL of *Ec. neotes* exceeds that of the majority of the *Ec. rendahli* material. Furthermore, HL/TL values of *Ec. rendahli* vexillifers (Fig. 57) do not fit the pattern observed for *Eu. owasianum*.

Onuxodon Smith

Onuxodon Smith, 1955: 406, type species, *Carapus parvibrachium* Fowler, 1927: 31, by original designation.

Growth Stages.—Three, corresponding to vexillifer, tenuis, and adult, although individuals referable to a compensatory (shrinking) tenuis stage are only presumed based on Figure 83.

Diagnosis: Adult.—Carapids lacking pelvic fins, elongate anal-fin radials, cardiiform teeth, a ventral patch of tunic ridges on the posterior swimbladder and thoracic plates formed by expanded parapophyses; and possessing a rockerbone, predorsal bone, numerous small distal radials supporting pectoral-fin rays, one to several large, symphyseal fangs on the premaxilla and dentary, facultative and/or obligatory commensal relationships with species of Mollusca (almost exclusively, see Table 6) and a unique larval morphology.

Diagnosis: Larvae.—Vexillifer larvae lacking ventral fins, cardiiform teeth, a visceral cradle and an exterilium gut; and possessing a vexillum placement adjacent to the first dorsal-fin ray and either anterior to or directly over a vertical through the anal-fin origin, VVO 4–8, D₃₀ 45–49, a simple proximal radial supporting the vexillum and secondarily the first dorsal ray, and a rockerbone (formed by 3.0–5.0 mm HL).

Comments.—Smith (1955a) erected the genus *Onuxodon* to accommodate Fowler's (1927) *Carapus parvibrachium*, a form Smith (1955a) considered "strikingly different." The distinctiveness of *O. parvibrachium* is partially evidenced by Fowler's (1927: 31) failure to recognize two additional specimens (figured and assigned by him to *Jordanicus caninus*) as closely related. The description of these last two

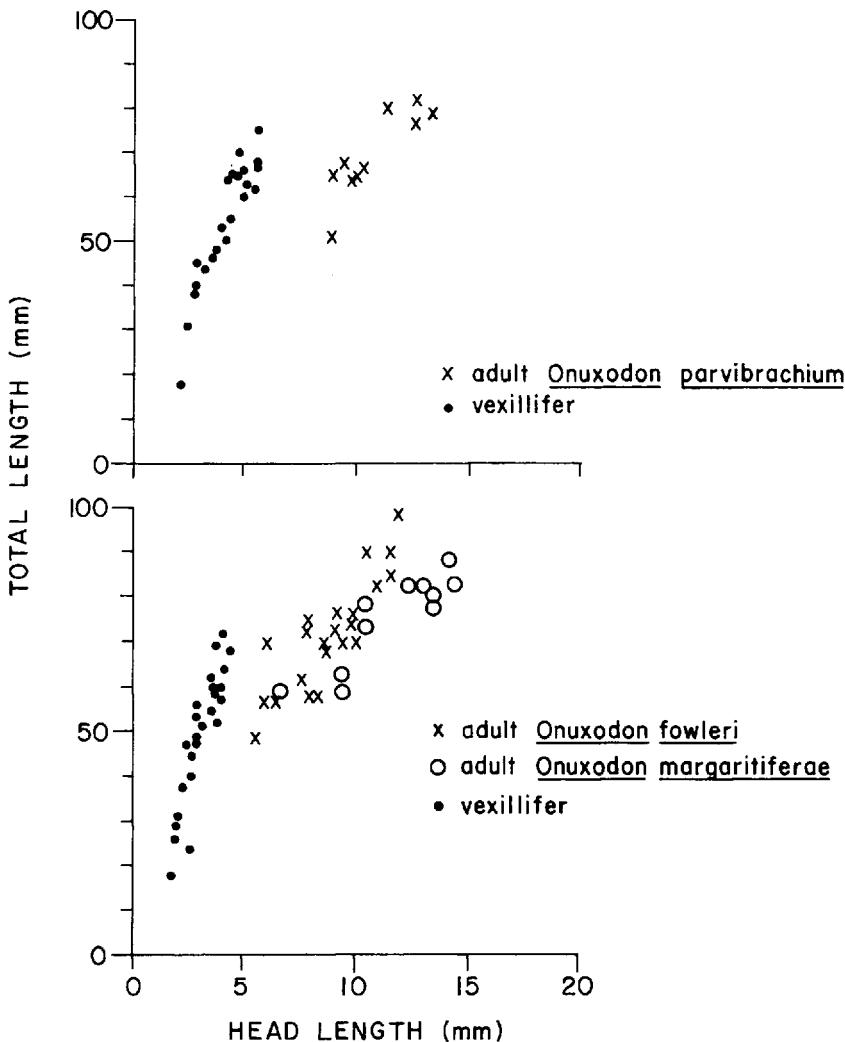


Figure 83. Total length versus head length relationship in *Onuxodon*: upper = *O. parvibrachium*; lower = *O. fowleri* and *O. margaritiferae*.

specimens (one of which is BPBM 5001) caused some concern to Smith (1955a: 403) in his evaluation of other carapine taxa and resulted in his designation of Fowler's (1927) *J. caninus* specimens as types of *Jordanicus fowleri* Smith, 1955 (type locality: Christmas Islands). The holotype of *Fierasfer margaritiferae* Rendahl, 1921 was one specimen in a large collection of pearlfishes taken from "Perlmuschein" in Western Australia (type locality: Cape Jaubert, south of Broome, Australia, 18.56°S, 121.39°E). Rendahl's (1921) type material, the holotype and multiple lots of paratypes, are deposited at NHRM, Stockholm. In addition, two paratypes are deposited in Copenhagen (ZMUC CN 11-12). *Carapus reedi* Smith 1955a: 410 (RUSI 296), described from Durban, is a juvenile *Onuxodon*, as suggested by Arnold (1956).

The geographical distributions of species of *Onuxodon* are presented below. Depth of capture ranges from about 1 to 30 m.

Table 13. Comparison of selected morphometrics in adults of three *Onuxodon* species (All except HL and TL (mm) expressed as a ratio to HL)

	<i>O. parvibrachium</i>				<i>O. fowleri</i>				<i>O. margaritiferae</i>			
	N	\bar{x}	Range	SD	N	\bar{x}	Range	SD	N	\bar{x}	Range	SD
HL	10	—	8.7-13.1	—	16	—	6.3-11.7	—	14	—	7.8-14.3	—
TL	10	—	51-82	—	16	—	57-99	—	14	—	58-83	—
SNL	10	0.2	0.2-0.3	0.02	16	0.2	0.2-0.2	0.02	14	0.2	0.2-0.2	0.02
ED	10	0.1	0.1-0.2	0.02	16	0.2	0.2-0.2	0.02	14	0.2	0.2-0.2	0.02
UJL	10	0.7	0.5-0.8	0.06	16	0.6	0.5-0.6	0.04	14	0.6	0.5-0.7	0.03
LJL	10	0.6	0.5-0.7	0.05	16	0.6	0.5-0.7	0.04	14	0.6	0.5-0.7	0.03
PDL	10	1.2	0.9-1.3	0.10	13	1.3	1.1-1.4	0.07	9	1.3	1.2-1.4	0.05
PAL	10	1.3	1.1-1.4	0.08	15	1.2	1.1-1.4	0.09	9	1.2	1.1-1.3	0.07
PL	10	0.2	0.2-0.2	0.04	16	0.5	0.3-0.5	0.06	10	0.4	0.3-0.5	0.04
HW	10	0.3	0.2-0.4	0.06	14	0.3	0.3-0.4	0.05	10	0.3	0.3-0.4	0.04
HD	10	0.7	0.6-0.7	0.02	16	0.6	0.6-0.8	0.06	10	0.6	0.5-0.8	0.08
BD	10	0.9	0.8-1.0	0.05	16	0.7	0.6-1.0	0.10	14	0.8	0.7-1.0	0.09
BI	10	0.2	0.1-0.2	0.03	14	0.2	0.2-0.2	0.02	10	0.2	0.1-0.2	0.03

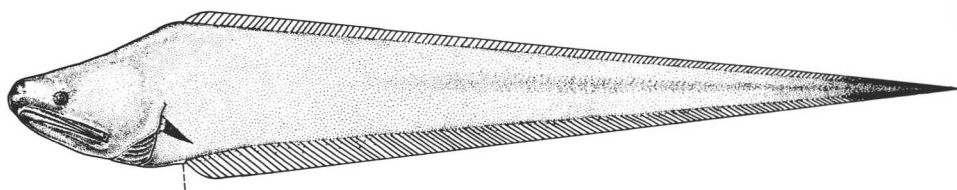


Figure 84. *Onuxodon parvibrachium*, WAM P26798-001, 12.4 mm HL.

Onuxodon parvibrachium (Fowler)
Figures 84, 85, 86

Carapus parvibrachium Fowler, 1927: 31, fig. 6 (Fiji I.).

Type Material Examined.—*Carapus parvibrachium*, PARATYPE, ANSP 91016, 13.9 mm HL, 70 mm TL, Suva Bay, Fiji, 21 June 1924, caught in a clam shell.

Other Material Examined: Adult.—8 lots; Pacific and Indian Oceans.

Other Material Examined: Larvae.—27 lots; Pacific and Indian Oceans.

Description: Adult.—Morphometric and meristic summaries are presented in Tables 4 and 13. Counts of the paratype are as follows: A_{30} 48, D_{30} 47, PCV 16, VDO 7, VAO 6, PDB 4–6, ARDO 2. The general appearance of *O. parvibrachium* is depicted in Figure 84. A detailed description and figure of the paratype is presented by Tyler (1970). Smith (1955a: 407) described colors in life. Color in alcohol white to brown.

Description: Larvae.—Morphometric and meristic variables of larval *O. parvibrachium* are presented in Tables 5 and 14. The general appearance of vexillifers is depicted in Figures 85 and 86. Larvae of *O. parvibrachium* were initially identified on the basis of the possession of a rockerbone, visible in cleared and stained material at about 4.5 mm HL (but see *O. fowleri*) and appearing as a small, bean-shaped mass (positive reaction to alcian blue in counter-stained specimens) anterior to the swimbladder. Vexillum position, ARDO and DRAO values (Table 5), selected morphometric variables, especially PDL (Table 14) and general morphology were used to construct a developmental series. In preserved material, pigment is restricted to 3–17 small melanophores scattered on the cranium, the number increasing with increasing HL. The gut is sac-like and bulbous and the vexillum is inserted anterior to the anal-fin origin (Figs. 85, 86) over vertebrae 4–6 (Fig. 39E).

Diagnosis: Adults.—A species of *Onuxodon* possessing a short pectoral fin (0.16–0.29 as a ratio to HL), small eyes (0.08–0.16 as a ratio to HL), PCV 16–18 and lacking lateralis papillae on the head or anterior lateral lines.

Diagnosis: Larvae.—*Onuxodon* vexillifers with a vexillum insertion anterior to a vertical through the anal-fin origin.

Comments.—Precaudal vertebrae in larvae (Table 5) exceed those of adults in a few cases and overlap with counts of adult *O. margaritiferae* (Table 4). In the smallest material, this discrepancy may be due to incomplete development of haemal spines, yet we recognize the potential for erroneous identification. No vexillifers of *Onuxodon* in our material, however, were collected in the area of Western Australia, the only known locality for *O. margaritiferae*. Resolution of this potential problem must await the positive identification of vexillifers of *O.*

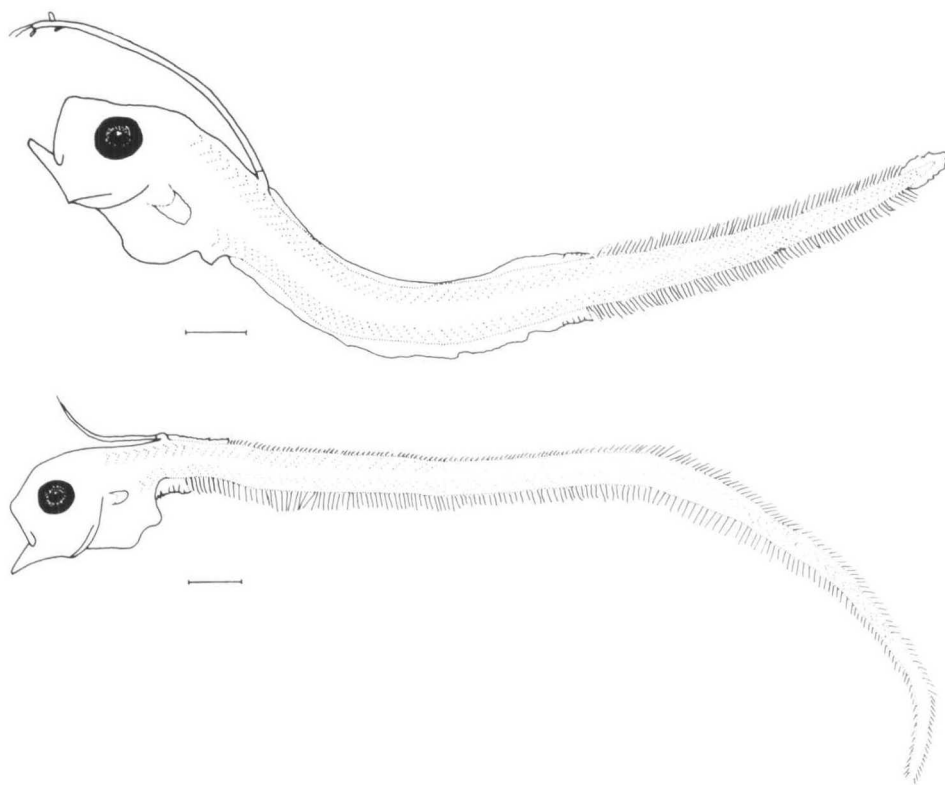


Figure 85. Upper—*Onuxodon parvibrachium*, ZMUC DANA 3731 III, 2.0 mm HL; Lower—*O. marginiferae*, ZMUC DANA 3665 IV, 1.8 mm HL.

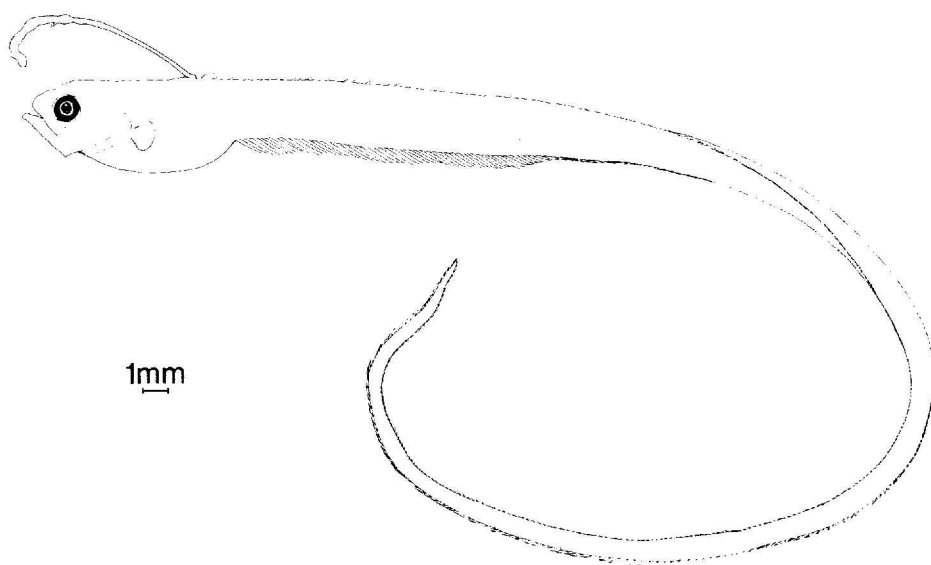


Figure 86. *Onuxodon parvibrachium*, ZMUC DANA 3768 XVI, 4.0 mm HL. Reproduced with permission from Gordon et al. (1984).

Table 14. Comparison of selected morphometrics in larvae of *Onuxodon fowleri* and *O. parvibrachium* (All values except HL and TL (mm) expressed as a ratio to HL)

	<i>O. fowleri</i>				<i>O. parvibrachium</i>			
	N	\bar{x}	Range	SD	N	\bar{x}	Range	SD
HL	14	—	1.9–4.4	—	13	—	2.5–5.4	—
TL	14	—	26–71	—	13	—	38–75	—
SNL	14	0.2	0.2–0.3	0.03	13	0.2	0.2–0.3	0.02
ED	14	0.3	0.2–0.3	0.02	13	0.2	0.2–0.3	0.02
UJL	13	0.5	0.5–0.6	0.02	13	0.5	0.4–0.5	0.03
LJL	14	0.6	0.5–0.6	0.04	13	0.5	0.5–0.6	0.02
VL	13	2.0	0.5–0.3	0.66	12	2.6	1.4–4.2	0.76
PVL	14	1.6	1.5–1.8	0.07	13	1.4	1.3–1.5	0.06
PDL	14	1.8	1.6–1.9	0.08	13	1.5	1.4–1.7	0.08
PAL	14	1.4	1.3–1.6	0.09	13	1.6	1.4–1.9	0.13
STA	13	1.4	1.3–1.4	0.04	13	1.5	1.4–1.8	0.11
HW	9	0.3	0.3–0.4	0.04	9	0.3	0.2–0.4	0.05
HD	13	0.7	0.6–0.8	0.08	12	0.7	0.6–0.9	0.06
BD	14	0.6	0.5–0.7	0.07	13	0.6	0.4–0.8	0.12
BI	8	0.2	0.1–0.2	0.02	8	0.2	0.1–0.2	0.03

margaritiferae. *Onuxodon* larvae superficially resemble those of some *Echiodon* species (see that genus account for details).

Our Hawaiian material of *O. parvibrachium* is restricted to larvae (Fig. 87), but we have been informed by Trott (pers. comm., 12 October 1983) that he has collected at least two adults from Puako on the Island of Hawaii. Reported hosts are listed in Table 6.

Onuxodon fowleri (Smith)
Figures 30, 88, 89, Plate 3

Jordanicus caninus: Fowler, 1927: 30, fig. 5 (Christmas I.).

Jordanicus fowleri Smith, 1955: 403 (based on *Jordanicus caninus* of Fowler, 1927; Christmas I.).

Carapus margaritiferae: various authors.

Onuxodon margaritiferae: various authors.

Type Material Examined.—*Jordanicus fowleri* LECTOTYPE, BPBM 5001, 9.0 mm HL, 73 mm TL, Whippoorwill Expedition, Christmas I., Line Is., August 1924, from pearl oyster. [We recognize as lectotype Fowler's (1927) specimen deposited in the Bishop Museum and as paralectotype Fowler's second specimen, present whereabouts unknown.]

Other Material Examined: Adult.—41 lots; Pacific and Indian Oceans.

Other Material Examined: Larvae.—34 lots; Pacific and Indian Oceans.

Description: Adult.—Morphometric variables are summarized in Table 13; those of the lectotype, expressed as a ratio to HL, are as follows (actual measurement in mm in parentheses): SNL 0.21 (1.9), ED 0.18 (1.6), UJL 0.58 (5.2), LJL 0.58 (5.2), PDL 1.28 (11.5), PAL 1.24 (11.2), STA 1.19 (10.7), PL 0.38 (3.4), HW 0.31 (2.8), HD 0.66 (5.9), BD 0.74 (6.7), BI 0.20 (1.8). Body depth of the holotype as a ratio to TL is 0.09. Meristic variables are summarized in Table 4, those of the lectotype as follows: A_{30} 48, D_{30} 47, PCV 20, VDO 6, VAO 5, VPB 4–6, ARDO 2. The general appearance of *O. fowleri* is depicted in Figure 88 and Plate 3. Color in life (Plate 3) is translucent. Chromatophores are conspicuous along the ventral margin associated with anal-fin radials, on the snout and brain and in a dark band associated with posterior vertebral centra. This latter pigment merges with dorsal and anal rays to produce a completely pigmented tail. Color in alcohol white to brown.

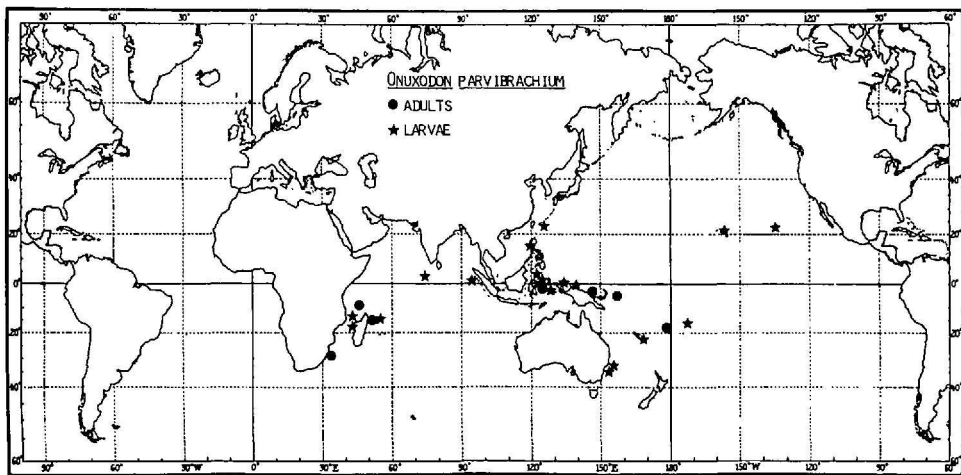


Figure 87. Distribution chart of *Onuxodon parvibrachium*.

Description: Larvae.—Meristic and morphometric variables of larval *O. fowleri* are presented in Tables 5 and 14. The general appearance of vexillifers is depicted in Figures 85 and 89. As with its congener, larvae were initially identified on the basis of the possession of a small, cartilaginous rockerbone visible in cleared and stained material by about 3.5 mm HL.

Diagnosis: Adult.—A species of *Onuxodon* possessing 19–22 precaudal vertebrae (modally 20), a relatively long and slender body (BD as a ratio to TL 0.06–0.10, \bar{x} 0.09) and distributed from South Africa and Indo-west Pacific localities to Hawaii.

Diagnosis: Larvae.—*Onuxodon* vexillifers with a vexillum insertion over or posterior to a vertical through the anal origin.

Comments.—Excluding *O. parvibrachium*, we found *Onuxodon* material to be variable relative to number of precaudal vertebrae, morphology and distribution (Fig. 90). Specimens from off Western Australia (types of *O. margaritiferae* and additional material) have lower precaudal vertebrae counts (Table 15), deeper bodies (Fig. 91) and different patterns of growth (Fig. 83). Specimens from all other localities (Fig. 90, including the lectotype of *O. fowleri*) have higher precaudal vertebral counts, more slender bodies and attain a larger TL at a smaller HL (Table 4, Figs. 83, 91). In a reasonably large sample ($N = 50$, Fig. 91), specimens of *O. fowleri* can be separated from *O. margaritiferae* on the basis of body depth as a function of TL (at TL greater than 55 mm).

Reported hosts are listed in Table 6. We can confirm two holothurian hosts,

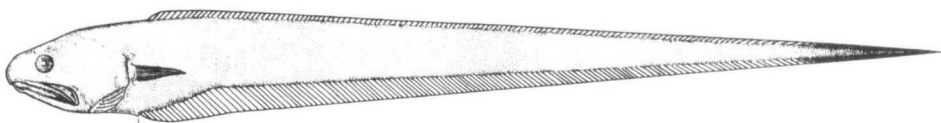


Figure 88. *Onuxodon fowleri*, OS 12486, 12.3 mm HL.

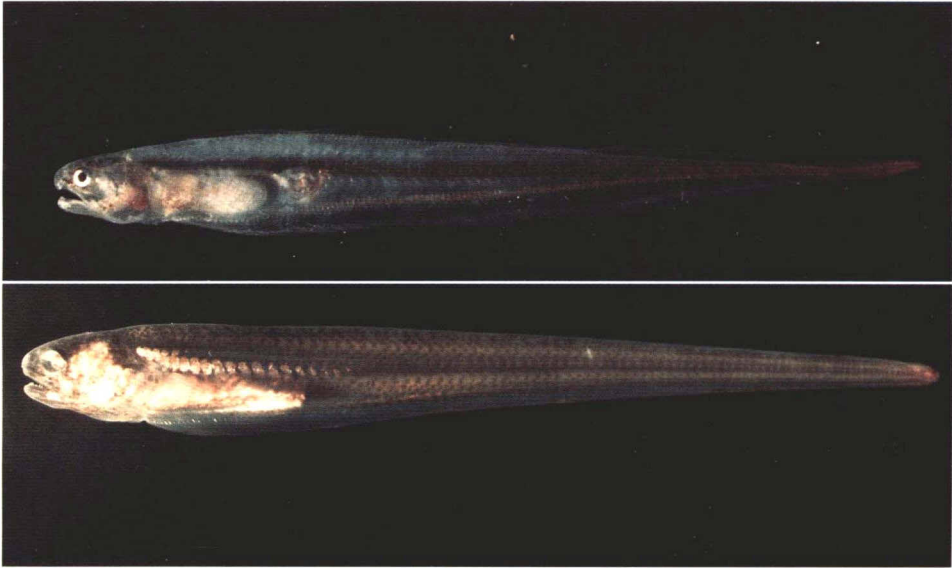


Plate 3. Upper—*Onuxodon fowleri*, BPBM 12325, 9.8 mm HL; Lower—*Carapus mourlani*, BPBM 12611, 19.8 mm HL. Photos by J. Randall.

one of which involved a juvenile (BPBM 25712, 9 mm HL) taken in *Thelenota ananas*, but such non-molluscan hosts are extremely rare.

Onuxodon margaritiferae (Rendahl)

Figure 92

Fierasfer margaritiferae Rendahl, 1921: 5 (off Cape Jaubert, Australia).

Type Material Examined.—*Fierasfer margaritiferae*, HOLOTYPE, NHRM MJO/1911.226.6888, 12.6 mm HL, 189 mm TL, Western Australia, Cape Jaubert, 45 naut. miles WSW, 70 ft, in pearl oyster, 3 June 1911, legit. Eric Mjoberg. *Fierasfer margaritiferae*, PARATYPES, NHRM MJO/1911.221.6894, 11.3–11.9 mm HL, Western Australia, Cape Jaubert, 42 naut. miles WSW, 70 ft, in pearl oyster, 29 May 1911. *Fierasfer margaritiferae*, PARATYPES?, ZMUC CN 11–12, 11.6–11.9 mm HL, 75–82 mm TL, legit. E. Mjoberg (Studiesamlingen), 45 miles WSW f. Cape Jaubert, of perlemuslinger. The ZMUC lot is dated 1.11. 1940 and does not bear the term “paratype.” The label, however, was apparently written by E. Mjoberg, cited by Rendahl (1921) as collector of this material. Additionally, the collection locality (45 mi west southwest of Cape Jaubert) is that of the NHRM types. We believe the ZMUC material may be part of the paratype series.

Other Material Examined: Adult.—5 lots; Western Australia.

Description: Adult.—Morphometrics are summarized in Table 13. Measurements (in mm) of the holotype are as follows: SL 2.3, ED 1.9, UJL 6.8, LJL 6.8, PAL 14.5, STA 14.4, PL 5.9, BD 8.7. Body depth expressed as a ratio to TL in 20 specimens (7.8–13.4 mm HL, 58–88 mm TL, 6.5–12.9 mm BD) ranged from 0.11–0.16 (\bar{x} 0.13, s_x 0.01, Fig. 91). Body depth as a ratio to TL in the paratypes is 0.11. Meristics are summarized in Tables 4 and 15, those of the holotype and ZMUC paratypes (in parentheses) as follows: A_{30} 51 (50, 51); D_{30} 49 (47, 46); PCV 19 (19, 19); VDO 7 (7, 7); VAO 6 (7, 6); VPB 4–6 (4–6, 5–6); ARDO 1–2 (0, 0). In addition, three NHRM paratypes possess 19 PCV. The general appearance of *Onuxodon margaritiferae* is depicted in Figure 92. Color in preservative is cream to tan. In the type series, the body lacks external melanophores except

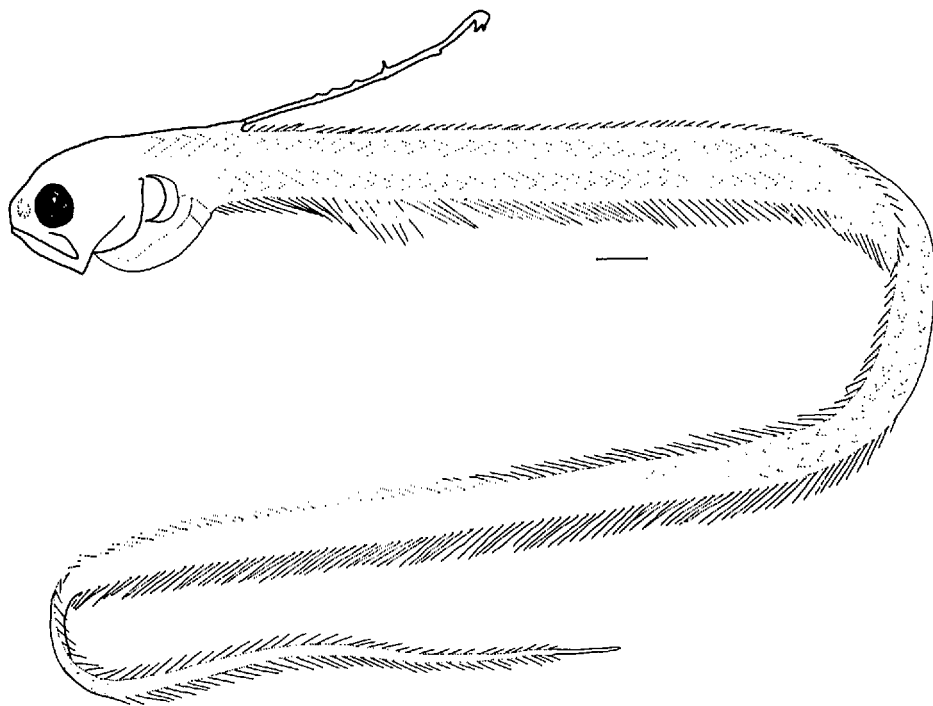


Figure 89. *Onuxodon fowleri*, ZMUC DANA 3689 IV, 2.7 mm HL.

for a dense scatter of stellate melanophores at the tail tip. Internal melanophores are visible through the cranium scattered over the hindbrain.

Description: Larvae.—No larval *Onuxodon* have been collected in the waters off Western Australia and the larva of *O. margaritiferae* is undescribed.

Diagnosis: Adult.—A species of *Onuxodon* possessing a long pectoral fin (0.33–

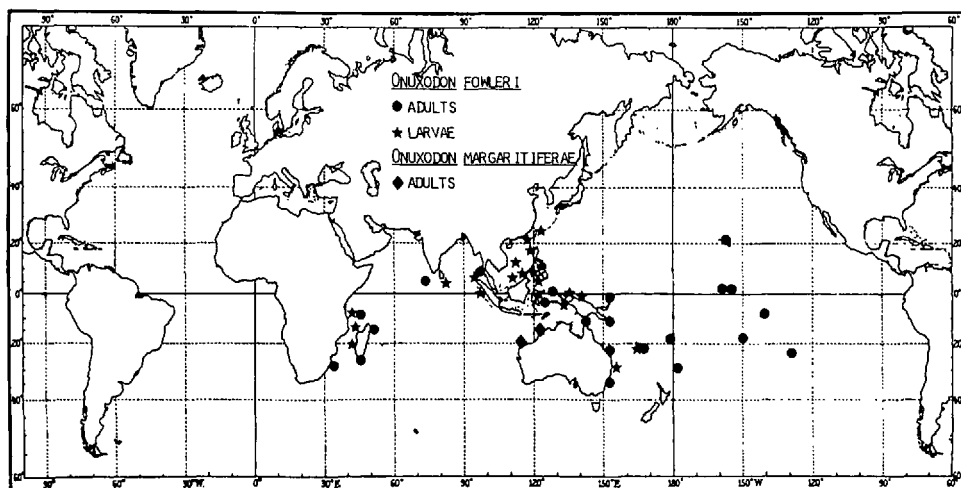


Figure 90. Distribution chart of *Onuxodon fowleri* and *O. margaritiferae*.

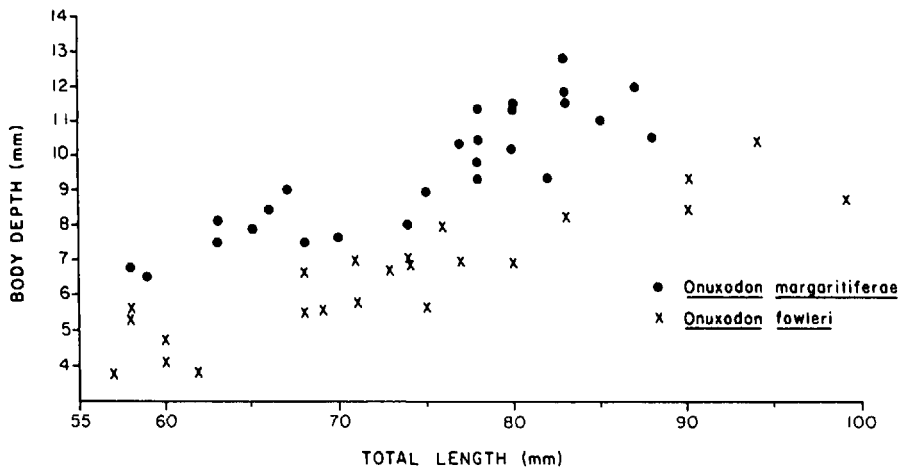


Figure 91. Body depth versus total length in *Onuxodon margaritiferae* and *O. fowleri*.

0.44 as a ratio to HL), PCV 18–20 (modally 19), a relatively short and deep body (BD as a ratio to TL 0.11–0.16, \bar{x} 0.13) and known only from off Western Australia.

Comments.—The only known host is the Western Australian pearl oyster (Table 6).

Carapus Rafinesque

Carapus Rafinesque, 1810: 57 (type species based on Opinion 42 of the International Commission on Zoological Nomenclature, 1942, *Gymnotus acus* Linnaeus).

Growth Stages.—Three, corresponding to vexillifer, tenuis and adult (Fig. 93).

Diagnosis: Adult.—Carapids lacking pelvic fins, rockerbones, enlarged dentary or premaxillary fangs, or diastemae; and possessing cardiform teeth (in all growth stages), facultative and obligatory commensal relationships with species of Holothuria, Asteroidea and Ascidiacea (Tables 6, 7), and a swimbladder constriction that delimits two subequal chambers.

Diagnosis: Larvae.—Vexillifer larvae lacking enlarged dentary and premaxillary teeth and possessing prominent cardiform teeth, an extremely elongate body resulting in a small HL/TL ratio, a ring of stellate melanophores located anterodorsal to the nasal rosette and a vexillum placement well anterior of the first

Table 15. Frequency distribution of precaudal vertebrae in three species of *Onuxodon*

PCV	<i>O. parvibrachium</i>	<i>O. margaritiferae</i>	<i>O. fowleri</i>
16	3		
17	7		
18	2	5	
19		23	2
20		4	30
21			18
22			3
Total	12	32	53



Figure 92. *Onuxodon margaritiferae* WAM P1316-60, 12.5 mm HL.

dorsal-fin ray, anterior to a vertical through the first anal-fin ray and posterior to a vertical through the base of the pectoral fin.

Comments.—Our interpretation of the larval morphology of the genus *Carapus* (Fig. 94) is complicated by the identification of only one larva (see the *Encheliophis dubius* section) in its sister genus, *Encheliophis*. In addition, only larvae of *C. acus* and *C. bermudensis* have been positively identified in *Carapus*, and these identifications are made possible only by collection locality.

A swimbladder bearing an intrinsic constriction is a unique specialization of *Carapus* (Figs. 31, 32 and see Characters and Polarity section) and the position of the constriction relative to vertebral centra is useful in species separation. In *C. mourlani*, the constriction is more anterior, lying under vertebrae 9–10, whereas in *C. acus* and *C. bermudensis* the constriction lies under vertebrae 11–12. In the holotype and only known specimen of *C. sluiteri*, the constriction lies under vertebra 13. In addition, these species differ in mean and modal pectoral-fin ray and precaudal vertebral counts, host preference and distribution (see key to *Carapus* species and accounts below).

The geographical distribution of *Carapus* species is shown in Figure 95 and of carapin larvae in Figure 96. Depth of capture ranges from less than 1 to 150 m.

Carapus acus (Brunnich)

Figures 31, 97, 98

Gymnotus acus Brunnich, 1768: 13 (Mediterranean Sea).

Carapus variegatus Fowler and Steinitz, 1956 (in part): 286, fig. 23 (Eilat, Israel).

Carapus birpex Arnold, 1956: 265, fig. 7 (Madeira).

Carapus cuspis Arnold, 1956: 267, fig. 8 (Madeira).

Synonymy and Neotype Designation.—Arnold (1956) believed Brunnich's (1768) type was no longer in existence, and the material is not listed among the carapid types at BMNH or MNHN-Paris (Wheeler and Bauchot, pers. comm.). Therefore, we designate the neotype described below. Fowler and Steinitz's (1956) description of *C. variegatus* includes non-type material obtained while dissecting holothurians

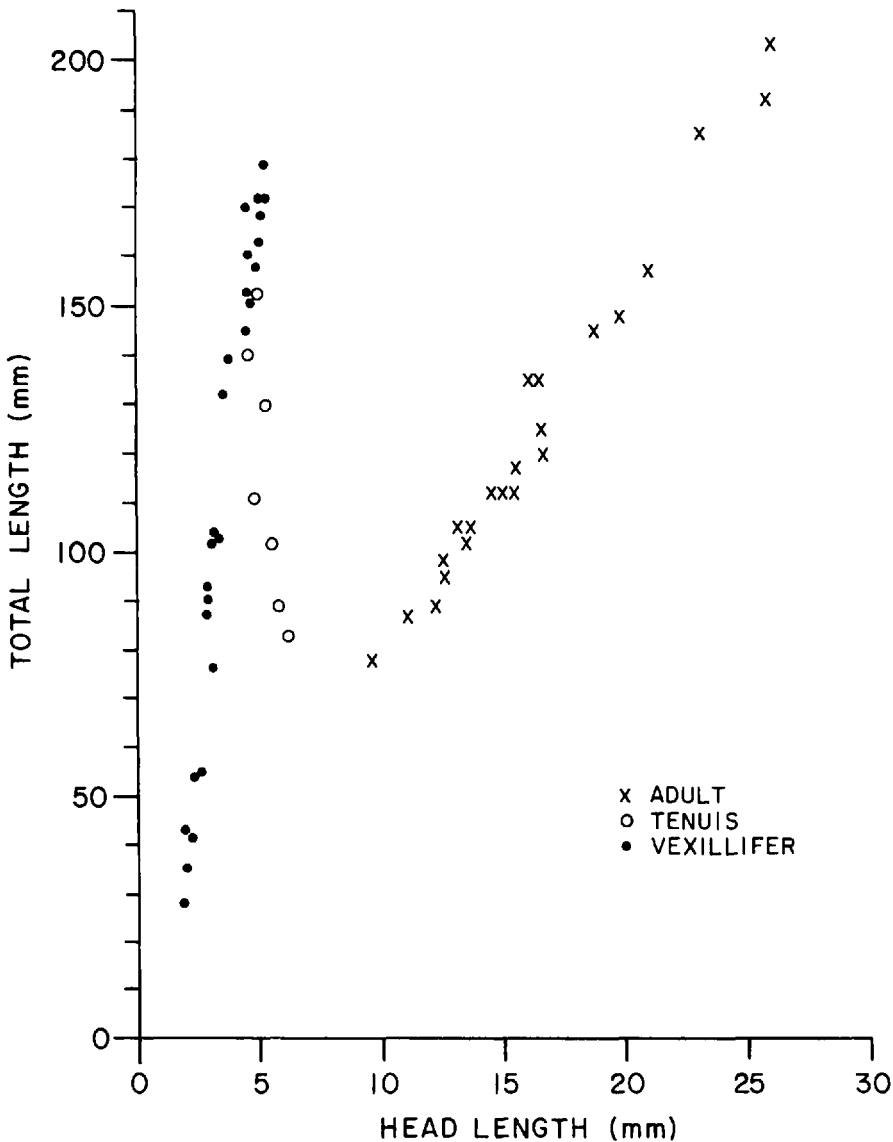


Figure 93. Total length versus head length relationship in *Carapus bermudensis*.

in Naples. We have not examined these specimens (HU 2010) but consider the collection referable to *C. acus* [see account of *C. mourlani* for synonymy of remaining Fowler and Steinitz (1956) material].

Type Material Examined.—*Carapus acus*, NEOTYPE, ZMUC Jour. No. 36, 19.7 mm HL, 161 mm TL, Palermo, Italy, identified by Doderlein, 12 I 1891. *Carapus birpex*, HOLOTYPE, MMF 2739, 28.8 mm HL, 208 mm TL, near Madeira, 30 VI 1942, precise locality and collector unknown (but see anecdotal data in Comments section), found in a holothurian. *Carapus cuspsis*, PARATYPE, BMNH 1954.5.3:1, 27.5 mm HL (measurement from radiograph), yacht PRINCESS ALICE, near Madeira, 33°02'N, 16°20'W, 100 m, 1897. *Encheliophis tenuis* Putnam 1874, HOLOTYPE, MCZ 12428, 5.7 mm HL, Mediterranean.

Other Material Examined: Adult.—33 lots; Mediterranean, eastern Atlantic and Ascension Island (a single specimen, ANSP 158791, 11.0 mm HL, see Comments) localities.

Other Material Examined: Larvae.—6 lots; Mediterranean localities.

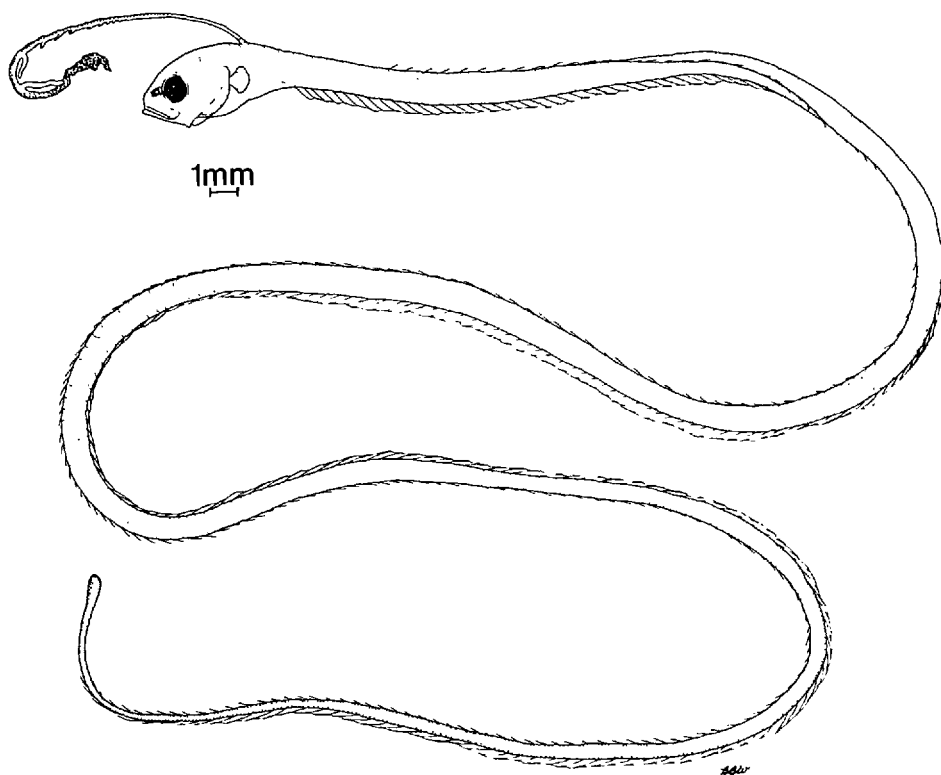


Figure 94. *Carapus/Encheliophis* sp., USNM uncat., 3.7 mm HL.

Description: Adult.—Measurements (mm) of the neotype are as follows: HL 19.7, TL 161, SL 3.3, ED 3.9, UJL 9.6, LJL 9.7, PDL 34.0, PAL 19.5, STA 18.5, PL 8.1, HW 6.3, HD 9.4, BD 11.0, BI 3.2, LTP 20.0. Meristic values of the neotype are as follows: A_{30} 60, D_{30} 38, PCV 18, VDO 12, VAO 3, ARDO 21, P_1 21. A morphometric comparison of eastern Atlantic, equatorial Atlantic and Mediterranean *C. acus* populations is presented in Table 16. In our very limited material, body size and proportions varied, especially HL, TL, ED, UJL, and PDL. Adults of *C. acus* collected near Madeira (MMF 2739, 21178, 14048, 14529, 8797) are large (ranges of HL and TL exceed all other material), have greater UJL values and usually possess larger eyes and greater PDL values (Table 16). Our sample sizes are small, however, and preclude an ability to delimit these populations based on morphometry. In addition, meristic comparison (Table 17) revealed overlapping ranges, although Mediterranean specimens tend to have lower mean values of PCV and A_{30} . Pigmentation variability was equally confusing in our material. Specimens range from unpigmented to highly pigmented (Fig. 97 and see photographs of living Mediterranean specimens in Gustato, 1976), and this variability appears unrelated to size, sex or length of preservation (one specimen, AMS B.6844, is highly pigmented after 100 years of preservation). In pigmented material, large stellate melanophores are distributed over the entire body (including dorsal-, anal- and pectoral-fin bases), the head, cheek, upper and lower jaws, snout tip, and laterally extending to the tail. Silver patches associated with myotomes are present abdominally and visible in specimens preserved for long periods of time.

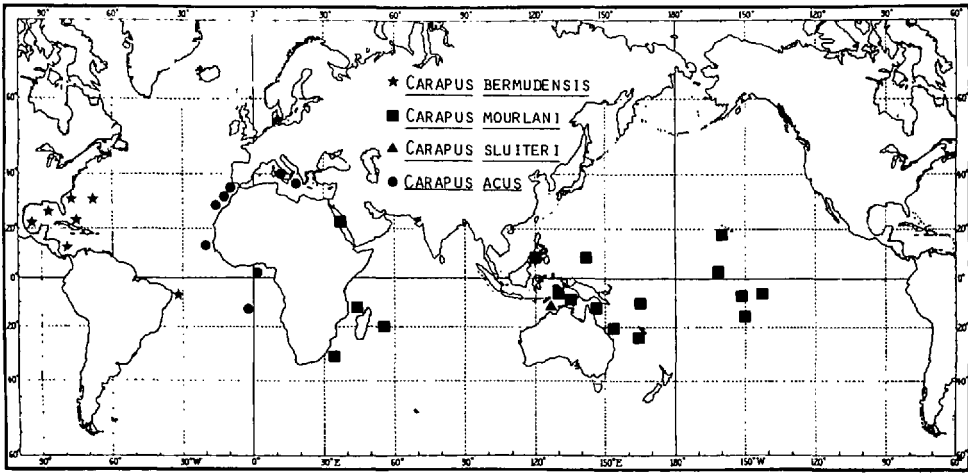


Figure 95. Distribution chart of *Carapus bermudensis*, *C. mourlani*, *C. sluiteri*, and *C. acus*; records of *C. mourlani* off India from Jones and Kumaran (1980) not shown.

The anterior half of the premaxilla bears an outer row of recurved cardiform teeth numbering 10–16 with totals increasing with increasing HL. Inner premaxillary teeth are short, conical, polyserial (about 3 rows) with the inner series being somewhat larger than outer rows at a large HL (20+ mm). At smaller sizes, inner premaxillary teeth are uniform in size tapering to a very small size posteriorly. The dentary bears an outer row of stout, conical teeth that are widely spaced posteriorly, becoming more numerous at the jaw tip. Inner dentary teeth are shorter, conical and somewhat polyserial (2–3 rows) but do not extend to the jaw tip. In juveniles (12 mm HL) teeth of the lower jaw are uniform in size. The adult pattern (inner polyserial teeth not extending to jaw tip) is apparent. The vomer bears a median patch of irregularly to uniformly spaced, large conical teeth that vary in number from one to many and are surrounded by smaller conical teeth. We observed considerable variability in vomerine dentition, both in number and pattern of teeth position. Smaller Mediterranean specimens possess fewer large,

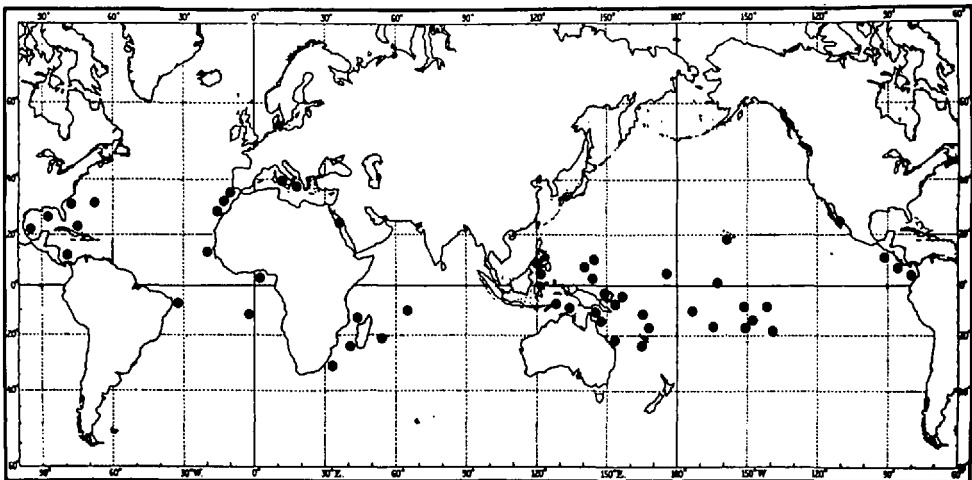


Figure 96. Distribution chart of larval Carapini.

Table 16. Morphometric comparison of three populations of adult *Carapus acus* (All values except HL and TL (mm) expressed as a ratio to HL)

	Off West Africa			Eastern Atlantic			Mediterranean		
	N	\bar{x}	Range	N	\bar{x}	Range	N	\bar{x}	Range
HL	5	—	11.7–23.0	5	—	28.8–34.9	5	—	13.8–24.8
TL	5	—	108–170	5	—	208–251	5	—	108–188
SNL	5	0.2	0.2–0.2	5	0.2	0.2–0.21	5	0.2	0.2–0.2
ED	5	0.2	0.2–0.2	3	0.2	0.2–0.23	5	0.2	0.2–0.3
UJL	5	0.5	0.4–0.5	5	0.5	0.5–0.56	5	0.5	0.5–0.5
LJL	5	0.5	0.8–0.5	5	0.5	0.5–0.56	5	0.5	0.5–0.5
PDL	3	1.5	1.5–1.6	3	1.8	1.6–1.8	4	1.7	1.6–1.7
PAL	5	0.9	0.9–0.9	4	0.9	0.9–1.0	5	0.9	0.9–0.9
STA	5	0.9	0.8–0.9	5	0.9	0.9–1.0	5	0.9	0.9–0.9
PL	5	0.5	0.4–0.5	5	0.4	0.3–0.47	5	0.5	0.4–0.5
HW	5	0.4	0.3–0.4	5	0.4	0.3–0.42	5	0.3	0.3–0.4
HD	5	0.5	0.4–0.5	5	0.5	0.4–0.54	5	0.4	0.4–0.5
BD	5	0.6	0.5–0.7	5	0.6	0.6–0.67	5	0.6	0.5–0.7
BI	5	0.1	0.1–0.2	5	0.2	0.2–0.17	5	0.2	0.1–0.2
LTP	5	1.0	1.0–1.1	4	1.1	1.0–1.1	5	1.0	1.0–1.0

median teeth that increase in number with HL (for example, 13 mm HL, one tooth; 18 mm HL, 4; 20 mm HL, 7). Larger eastern Atlantic specimens possess more and larger median teeth (7–10) arranged in varying patterns from uniformly spaced in a median row to irregularly spaced (see Arnold, 1956: 266, his fig. 8). Palatine teeth are small, conical, polyserial and decrease in size and number posteriorly.

Swimbladder possesses two pseudo-chambers separated by a constriction under vertebrae 11–12.

Description: Larvae.—The material contains 12 vexillifer and four tenuis larvae, all identified on the basis of distribution. The majority of these specimens are in poor condition. Ranges of morphometric variables (expressed as ratio to HL) of two vexillifer (MCZ 70116, 4.7 mm HL, 180 mm TL; ZMUC, 3.1 mm HL, 65 mm TL, see Fig. 98) and two tenuis larvae (ISH 1031/64, 8.6 mm HL, 205 mm TL; ISH 382/64, 8.7 mm HL, 224 mm TL) are as follows, vexillifers listed first: SNL 0.23–0.29, 0.24–0.26; ED 0.21–0.23, 0.17–0.18; UJL 0.45–0.46, 0.44–0.45; LJL 0.52–0.53, 0.46–0.50; PDL 2.00–2.29, 1.68; PAL 1.29, 1.10–1.15; STA 1.23–1.26, 1.05–1.09; PL 0.13, 0.20–0.24; HD 0.70–0.77, 0.40–0.47; BD 0.45–0.47, 0.43–0.58.

Counts of P_1 , ARDO, VDO and VAO in both vexillifer and tenuis larvae fall

Table 17. Comparison of selected meristics in three populations of *Carapus acus*

	Mediterranean			Eastern Atlantic			Off West Africa		
	N	Range	\bar{x}	N	Range	\bar{x}	N	Range	\bar{x}
A ₃₀	7	55–60	57.1	6	60–63	61.0	9	58–63	60.6
D ₃₀	6	36–39	37.7	5	37–44	39.4	8	36–43	40.4
PCV	7	17–18	17.7	6	18–19	18.3	9	17–19	18.1
VDO	6	11–13	12.2	5	11–13	11.9	8	10–13	11.2
VAO	7	2–4	3.1	6	3–4	3.4	9	1–3	2.2
ARDO	6	18–23	20.7	5	21–25	22.4	8	19–22	20.8
P ₁	8	20–24	21.4	7	21–24	22.0	15	20–23	21.3

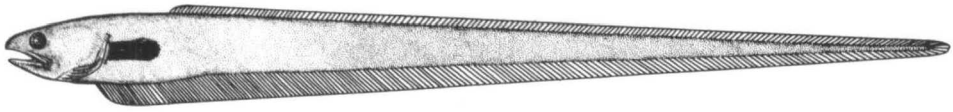


Figure 97. *Carapus acus* (holotype of *C. birpex*), MMF 2739, 28.8 mm HL.

within ranges of adults. Vexillifers (Fig. 98) are unpigmented and are similar in appearance to other known *Carapus* vexillifers (see genus account). Tenuis larvae are also unpigmented and similar in appearance to tenuis stages of *C. bermudensis*. The HL/TL relationship is presented in Figure 99. A swimbladder with two pseudo-chambers is not developed in the size range of tenuis larvae available, and the size at which this adult feature develops is unknown (see Comments section in regard to an Ascension I. specimen).

Diagnosis: Adult.—A holothurian-inhabiting species of *Carapus* possessing a free, movable maxilla; swimbladder with two pseudo-chambers separated by a constriction under vertebrae 11–12; and P₁ 20–24. The species is distributed along eastern shores of the Atlantic and the Mediterranean Sea and probably south to Ascension I. (see Comments section).

Comments.—Arnold (1956) considered records of *C. acus* collected outside the Mediterranean as doubtful and, partly on the basis of these distributional data, erected *C. birpex* and *C. cuspis*. Arnold (1956: 268–269) discussed dentition, size and form of maxillae, head proportions and absolute size as diagnostic characters delimiting these forms. We are unable to separate the material using these characters.

Depth distribution data for *C. acus* in the eastern Atlantic are sparse. Our characterization of this population as “deep-dwelling” is based on the occurrence of three specimens as stomach contents of *Aphanopus carbo* (MMF 14047, 14048

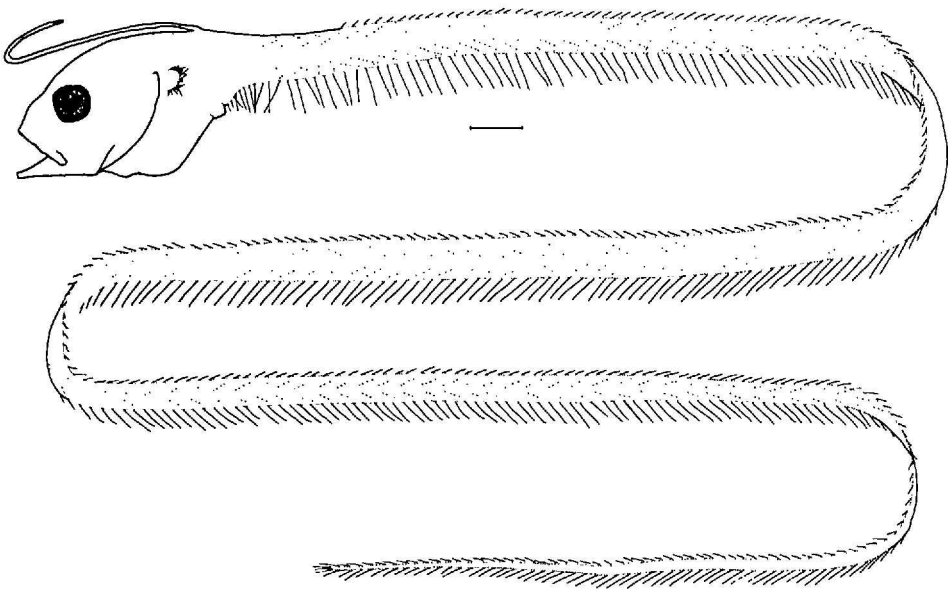


Figure 98. *Carapus acus* ZMUC DANA 1123 III, 3.1 mm HL.

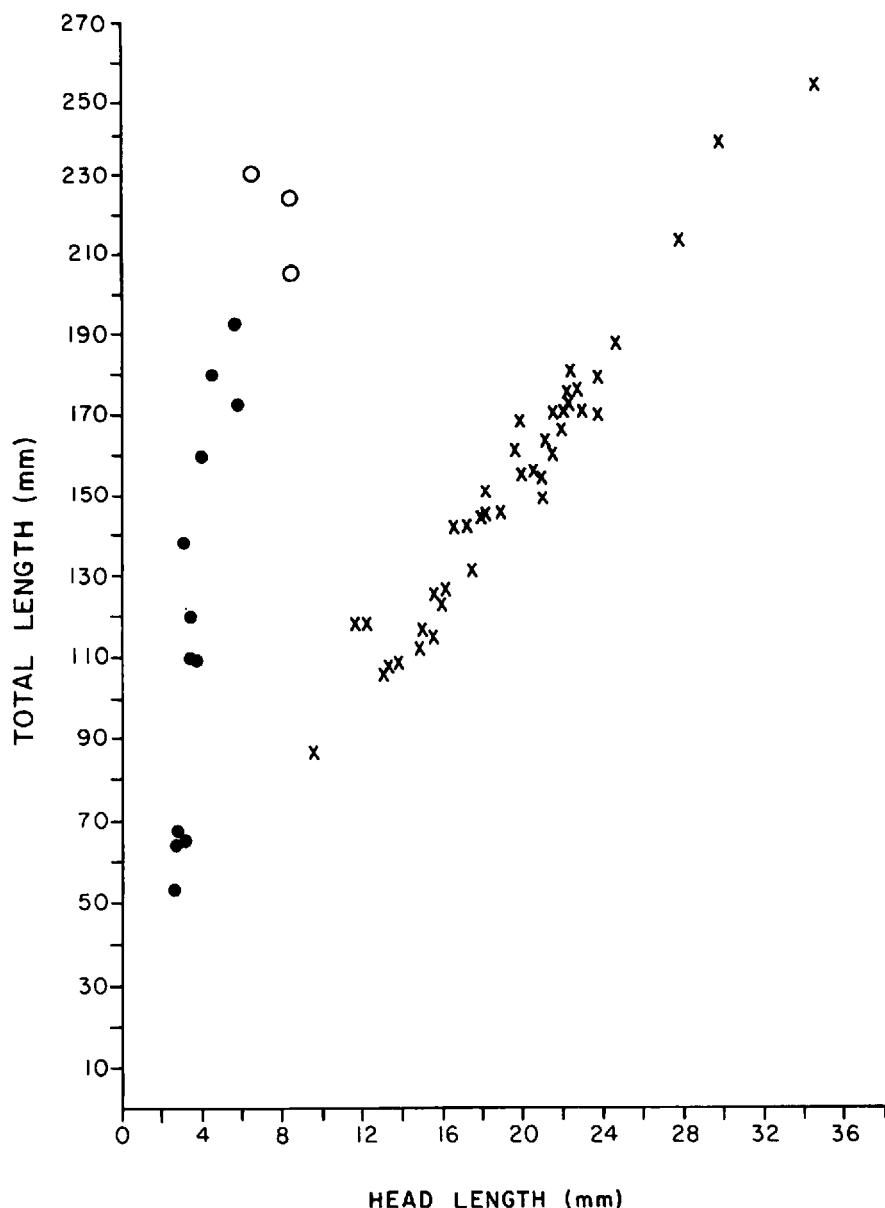


Figure 99. Total length versus head length relationship for *Carapus acus*.

and 14529) as well as the deep capture record (100 m) for the paratype of *C. cuspis*. Two additional specimens, however, were found in guts of *Conger conger* (MMF 21178, 8797), and the holotype of *C. birpex* was probably collected in the Bay of Funchal in nearshore depths of 20–30 m (G. E. Maul, pers. comm., 31 July 1987), as the holotype was one of three specimens taken in an unidentified holothurian and brought to MMF by fishermen. It is likely that the additional specimens were discarded by the collectors.

A single, transforming specimen (11.0 mm HL, 110 mm TL; ANSP 158791) with 21–22 pectoral rays but without an intrinsic swimbladder constriction was collected in deep water off Ascension Island. This specimen represents the only

Table 18. Morphometric comparison of tenuis and adult specimens of *Carapus bermudensis* (All values except HL and TL (mm) expressed as a ratio to HL)

	Tenuis				Adult			
	N	\bar{x}	Range	SD	N	\bar{x}	Range	SD
HL	10	—	4.6–6.3	—	12	—	13.7–26.1	—
TL	10	—	111–371	—	12	—	105–197	—
SNL	10	0.3	0.3–0.3	0.01	12	0.2	0.2–0.2	0.01
ED	10	0.2	0.2–0.2	0.02	12	0.2	0.2–0.2	0.02
UJL	10	0.4	0.4–0.5	0.02	12	0.5	0.5–0.5	0.01
LJL	10	0.5	0.5–0.5	0.03	12	0.5	0.5–0.5	0.02
PDL	1	—	1.8	—	11	1.6	1.6–1.7	0.05
PAL	10	1.3	1.1–1.4	0.13	12	0.9	0.9–1.0	0.06
PL	9	0.2	0.1–0.2	0.04	12	0.5	0.4–0.5	0.03
HW	10	0.3	0.2–0.3	0.03	12	0.4	0.3–0.4	0.02
HD	10	0.5	0.5–0.5	0.02	12	0.5	0.5–0.5	0.02
BD	10	0.5	0.4–0.6	0.06	12	0.6	0.5–0.7	0.05
BI	10	0.2	0.1–0.2	0.02	12	0.2	0.1–0.2	0.01
LP	10	1.0	1.0–1.0	0.02	12	1.0	0.8–1.1	0.07

occurrence below 20°S for this species as well as the first record of a pearlfish from Ascension Island. Further collection is warranted to clarify the status of this population.

Carapus bermudensis (Jones)

Figures 23, 31, 100, Plate 2

Lefroyia bermudensis Jones, 1874: 3837 (Bermuda I.).

Fierasfer dubius (in part) Putnam, 1874: 343 (Atlantic specimens only).

Carapus recifensis Ancona-Lopez, 1956: 390, fig. 1 (off Recife, Brazil).

Carapus chavesi Ancona-Lopez, 1956: 392, fig. 2 (off Recife, Brazil).

Type Material Examined. — *Lefroyia bermudensis*, HOLOTYPE, USNM 23807, 15.5 mm HL, Gov. Lefroy, Bermuda. The holotypes of *C. recifensis* and *C. chavesi* Ancona-Lopez, 1956 are not deposited in MZUSP and are presumed lost (N. Menezes, in litt., 12 Oct. 1984). Putnam (1874) included five specimens collected at Atlantic localities in his designation of cotypes of *Fierasfer dubius*. These specimens, as noted by Jordan and Evermann (1898) and Arnold (1956) are referable to *C. bermudensis*, based on distributional and host records. We did not examine this material but noted the museum number and number of specimens as follows: MCZ 12424(1), MCZ 12425(1), MCZ 12426(1), MCZ 12427(1), MCZ 12430(1). The sixth specimen (Agassiz Coll. No. 4334) is missing from the MCZ collections.

Other Material Examined: Adult. — 19 lots; Atlantic localities.

Other Material Examined: Larvae. — 61 lots; Atlantic localities.

Description: Adults. — Morphometric variables are summarized in Table 18. Meristic ranges based on examination of 28 specimens are as follows, those of Jones's (1874) type in parentheses: A_{30} 53–62 (56), D_{30} 36–45 (39), PCV 17–18 (18), VDO 10–14 (11), VAO 2–4 (3), ARDO 17–25 (19), P_1 17–20. The general appearance of *C. bermudensis* is presented in Figure 100. Color in life is translucent (Plate 3) with silvery bands (Trott, 1970 reports 12 in number) along flanks; pigmented vertebral column conspicuous; cheek with silver patch (Trott, 1970) and large erythrophores on dorsal and anal bases (Trott, 1970). Color in preservative tan. Melanophore distribution somewhat variable in our material. The largest specimens (20–26 mm HL) are the most highly pigmented with large stellate melanophores scattered on the cheek, at the pectoral-fin base and along the entire lateral aspect of the trunk and tail except over the gut. Dorsally, large melanophores are grouped in saddles which appear in series from the nape of the neck to the tail tip. Dorsal and lateral pigment merge posteriorly, and the entire posterior

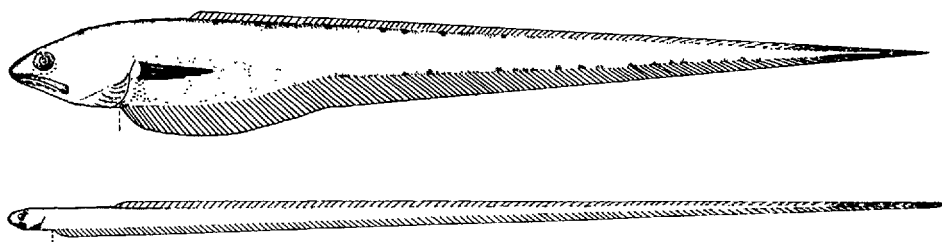


Figure 100. Upper—*Carapus bermudensis*, AMNH 37388, 16.5 mm HL. Lower—*C. bermudensis*, tenuis stage, AMNH 37388, 5.8 mm HL.

third of the tail is covered with dark melanophores. In smaller specimens (up to approx. 17 mm HL), external pigment of the trunk and tail is generally confined to the dorsal- and anal-fin bases (Fig. 100), and these pigment patterns merge over the posterior third of the tail. In addition, melanophores are visible at the snout tip and on the upper jaw. In adult material of all sizes, internal melanophores are visible covering the brain; scattered on the abdominal wall, becoming darker dorsally above the swimbladder; and associated with the vertebral column.

Teeth on the premaxilla are small, conical and polyserial. The innermost teeth on the anterior third are larger, less tightly spaced and somewhat recurved. There is an outer row of 6–10 cardiform teeth on anterior third of premaxilla. The palatine teeth are short, blunt, conical and gradually become smaller posteriorly. An outer row of sharp conical teeth on dentary are longer than largest premaxillary teeth. The inner dentary teeth are short, blunt and polyserial. The vomer has a median row of large stout teeth, ranging from 5–9 in number, and flanked by a single row of short blunt teeth.

There are no lateral line scales. The haemal spines are only partly spatulate and the anterior swimbladder chamber is separated from the posterior chamber by a conspicuous constriction under vertebrae 11–12.

Description: Larvae.—Vexillifer and tenuis larvae of *C. bermudensis* are identified and illustrated in Olney and Markle (1979) and Figure 100. Counts on three cleared and stained tenuis larvae (AMNH 23561: 4.6, 4.7, 4.9 mm HL) are as follows: A_{30} 53–58, D_{30} 39–42, VVO 4–5, VDO 10–11, VAO 6–7, PCV 17–18, ARDO 13–18, P_1 19. An accessory cartilage is present anterior to the second neural spine. The modified radial that supported the larval vexillum is present over vertebrae 3–5. Vexillifer and tenuis larvae are sparsely pigmented. Melanophores are only visible on the nasal rosette, scattered on the dorsal- and anal-fin bases at the tail tip, and, internally, dorsal to the developing swimbladder and scattered on the brain. A morphometric comparison of tenuis and adult specimens is presented in Table 18.

Diagnosis.—A holothurian-inhabiting species of *Carapus* with a free, movable maxilla; swimbladder with two pseudo-chambers separated by a constriction under vertebrae 11–12; PCV 17–18 and P_1 17–20.

Comments.—The species is distributed along the western shores of the Atlantic Ocean, Bermuda and the Caribbean Sea south to Brazil. Despite widespread distribution of pelagic larval stages of *Carapus/Encheliophis* (Fig. 96) and the potential for exchange between western and eastern Atlantic populations of *Carapus*, we consider *C. acus* and *C. bermudensis* as separate taxa which can be distinguished by numbers of pectoral-fin rays.

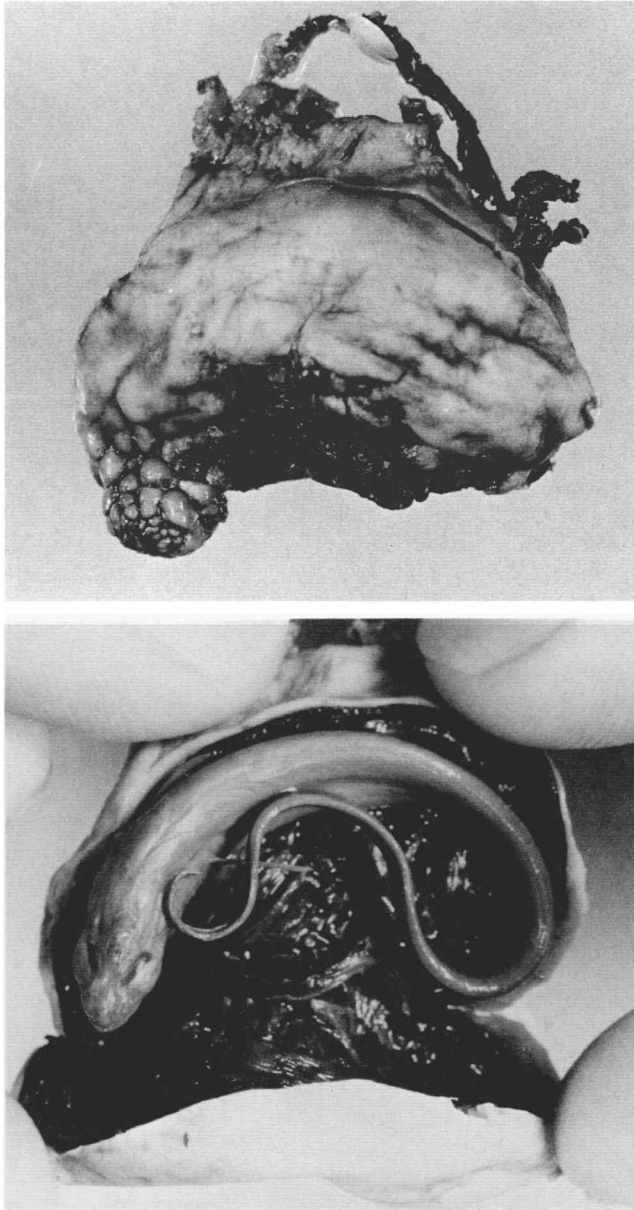


Figure 101. *Carapus sluiteri*: Upper—Ascidean host of holotype; Lower—holotype, ZMA 112.679, 13.8 mm HL, as found and preserved in host.

Carapus sluiteri (Weber)
Figure 101

Fierasfer sluiteri Weber, 1913: 97, fig. 8 (off Timor I., Indonesia).

Type Material Examined.—*Fierasfer sluiteri*, HOLOTYPE, ZMA 112.679, 13.8 mm HL, 100 mm TL (from Weber, 1913), female, Indonesia: southeast of Timor, 08°39.1'S, 127°04.4'E, 34 m, Siboga Exp. Sta. 285, 18 I 1900.

Other Material Examined.—ZMA 112.680, 7.3 mm HL, 60 mm TL, collected near the holotype at Siboga Expedition station 299, 10°52.4'S, 123°01.1'E; 34 m, 27–29 I 1900.

Description: Adult.—Morphometric variables expressed as a ratio to HL of the holotype are as follows, actual measurements (mm) in parentheses: SNL 0.17 (2.4); ED 0.23 (3.2); UJL 0.49 (6.7); LJL 0.48 (6.6); PDL 1.53 (21.1); PAL 0.98 (13.5); STA 0.91 (12.6); PL 0.47 (6.5); HW 0.38 (5.2); HD 0.41 (5.6); BD 0.54 (7.4); BI 0.14 (1.9); LTP 1.02 (14.1). Meristic data from the holotype are presented in Table 4. The general appearance of the holotype (and only known specimen) and its host are presented in Figure 101. Color in alcohol is tan. Approximately 12 very faded, silver patches are visible laterally and are associated with abdominal myotome segments. In addition, two larger silver patches (also faded) are visible on the operculum. The remainder of the body appears unpigmented with the exception of large stellate melanophores covering the brain and scattered on the snout.

The maxilla is free, movable, not covered by skin and toothless. The premaxilla bears an outer row of cardiform teeth. The inner premaxillary teeth are small, blunt, conical and polyserial, those of the jaw tip larger and somewhat curved. The dentary teeth are short, conical and polyserial, those of outer rows somewhat larger. The palatine teeth are short, blunt, conical, and polyserial. The vomer has five stout median teeth surrounded by small, blunt conical teeth. Both dentary bones are broken.

The anterior swimbladder chamber (Fig. 32) is separated from the posterior chamber by a conspicuous constriction under thoracic vertebra 13.

Description: Larvae.—Larval stages of *C. sluiteri* are unknown.

Diagnosis.—An ascidian-inhabiting species of *Carapus* with a free, movable maxillary; a swimbladder possessing two pseudo-chambers and 19 PCV.

Comments.—Weber (1913) reported the ascidian host of *C. sluiteri* as a species of *Styela* and included a second specimen (ZMA 112.680) in his brief description. The specimen possesses 19 PCV and a dentary pattern similar to the holotype. Identification of this individual, however, is problematic since the swimbladder is damaged and the specimen was collected in the bivalve *Cardium* (Weber, 1913). The specimen is not referable to *Onuxodon* since it lacks a rockerbone. Another molluscan-inhabiting species, *E. dubius*, possesses 19–21 PCV, a simple swimbladder and may have an extended range (see *E. dubius*). Until additional material of this rare pearlfish is available, the extent to which *C. sluiteri* utilizes non-ascidian hosts is unknown. As a result, we are unable to confidently identify Weber's (1913) second specimen.

Carapus mourlani (Petit)
Figures 12, 31, 102, Plate 3

Oxybeles lumbricoides Bleeker, 1854: 163 (Ceram I., Indonesia)—*nomen dubium*.

Fierasfer mourlani Petit, 1934: 393 (Madagascar I.).

Carapus pindae Smith, 1955a: 412, fig. 7 (Mozambique).

Carapus mayottae Smith, 1955a: 415, fig. 8 (Comoros Is.).

Carapus variegatus Fowler and Steinitz, 1956 (in part).

Synonymy and Neotype Designation.—Neither Bleeker's (1854) type of *O. lumbricoides* nor Petit's (1934) type of *F. mourlani* are listed in the collections of BMNH or MNHN-Paris (Alwyne Wheeler, in litt., 24 March 1982; M. L. Bauchot, in litt., undated). Bleeker's (1854) type is presumed lost (M. J. P. van Oijen, in litt., 18 Oct 1985), and the disposition of Petit's (1934) type is unknown. As noted by Schultz (1960), Bleeker's description is inadequate and does not permit meristic or anatomical comparison with available material. His specimen was collected in Ceram (Indonesia), probably from

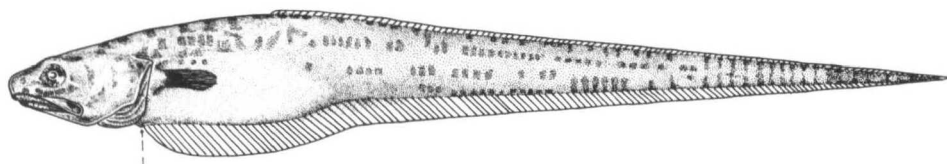


Figure 102. *Carapus mourlani*, neotype, ZMUC uncat., 19.8 mm HL.

Culcita. This host record is tentative and we consider Bleeker's (1854) name a *nomen dubium*. Petit's (1934) description of a single specimen taken from *Culcita* at Sarodrano (south of Tulcar, Malagasy Republic) is clearly referable to *C. mourlani* on the basis of host record and pigmentation. Notwithstanding the uncertainty of the whereabouts of Petit's type, we designate the neotype described below and illustrated in Figure 102. The neotype was collected along with additional specimens in starfish off Cannonier's Pt., Mauritius, near Petit's type locality.

Additional synonymy is based on examination of type material. It should be noted that Fowler and Steinitz's (1956) description of *C. variegatus* includes material (non-type) obtained while dissecting holothurians in Naples. These specimens (HU 2010) have not been examined but are most probably referable to *C. acus* (see *Carapus acus*).

Type Material Examined.—*Carapus mourlani*, NEOTYPE, ZMUC, 19.8 mm HL, 128 mm TL, Dr. Thor Mortensen's Java—S. Africa Exp., Cannonier's Pt., Mauritius, 18 Sept. 1929, from *Culcita*. *Carapus pindae*, HOLOTYPE, RUSI 334, 10.7 mm HL, 74 mm TL, Baixo Pinda, 14°10'S, 40°40'E, July 1955, inside large holothurian. *Carapus variegatus*, HOLOTYPE, ANSP 72145, 14.5 mm HL, H. Steinitz, Eilat, Israel, 23 IV 1951, obtained in holothurians. *Carapus variegatus*, PARATYPES, ANSP 72146 and 72147, 11.9 and 8.5 mm HL, same data as holotype. *Carapus mayottae*, HOLOTYPE, MNHN 1892.666 A5107, 12.9 mm HL, Vimont, Mayotte I., Comoros Is.

Other Material Examined: Adult.—51 lots; Pacific, Indian Ocean and Red Sea localities.

Description: Adult.—Mean, range and standard deviation of morphometrics in 17 specimens (10.0–25.8 mm HL, 65–170 mm TL) are as follows, values expressed as a ratio to HL: SNL 0.17, 0.16–0.19, 0.01; ED 0.18, 0.15–0.22, 0.02; UJL 0.46, 0.43–0.62, 0.05; LJL 0.48, 0.44–0.58, 0.03; PDL 1.71, 1.57–1.92, 0.08; PAL 0.92, 0.86–1.00, 0.05; PL 0.39, 0.33–0.47, 0.04; HW 0.39, 0.30–0.50, 0.04; HD 0.51, 0.45–0.55, 0.03; BD 0.62, 0.49–0.69, 0.07; BI 0.17, 0.14–0.18, 0.01. Ranges of meristic data for 41 specimens are as follows, those of the neotypes in parentheses: P₁ 17–21 (19, 20), A₃₀ 54–61 (56), D₃₀ 35–41 (38, 38), PCV 15–17 (15, 16), VDO 11–14 (12, 13), VAO 2–4 (2), ARDO 18–25 (22). The general appearance of *C. mourlani* is illustrated in Figure 102. Color in life (Pl. 3) is translucent and highly pigmented with 19–26 (Trott, 1970) silver patches associated with abdominal myotome segments. Color in preservative is variable, pale to dark brown. Lateral silver patches are only visible in freshly preserved material. Large stellate melanophores are conspicuous and scattered over the entire body except the dorsal, anal and pectoral fins and the abdominal region.

The anterior half of premaxilla has an outer row of cardiform teeth. Inner premaxillary teeth are conical, polyserial and densely packed. Tip of premaxillary with 1 or 2 large conical teeth which are somewhat recurved. The inner dentary teeth are small, conical and polyserial. An outer row of dentary teeth are large conical and somewhat curved. This single row gradually increases in size proceeding anteriorly and grades into a patch of smaller teeth at the lower jaw tip. The palatine teeth are short, stout, conical and polyserial. The vomer has 2–3 large, stout median teeth surrounded by small, blunt conical teeth. In the rear of the vomer is a small patch of conical teeth of intermediate size.

The otoliths have scalloped edges (Trott, 1970) and apparently variable morphology. Accessory cartilage present. Neural and haemal spines are spatulate. The anterior swimbladder chamber is separated from the posterior chamber by a

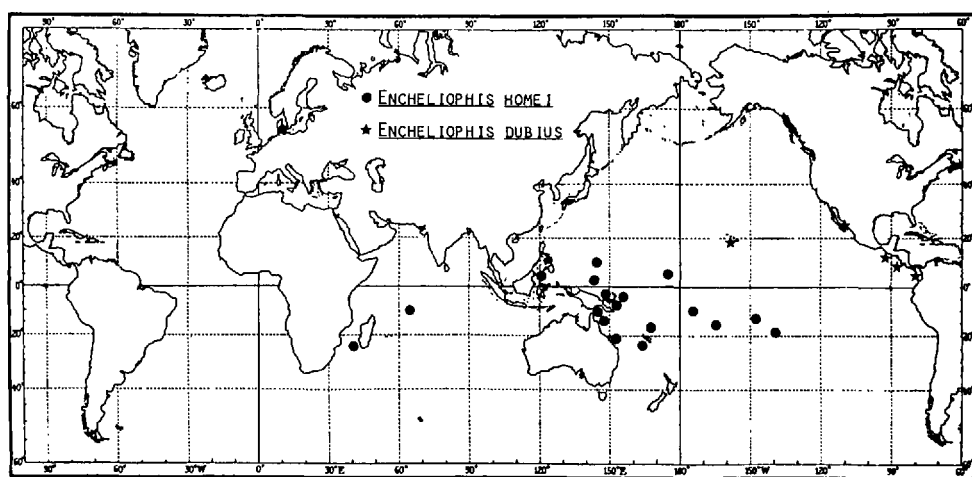


Figure 103. Distribution chart of *Encheliophis homei* and *En dubius*.

conspicuous constriction under thoracic vertebrae 9–10. The lateral line canal is conspicuous.

Description: Larvae.—The vexillifer of *C. mourlani* is undescribed. Two tenuis larvae (BPBM 25187, 8.4 and 9.6 mm HL) were collected from the coelom of *Culcita novaeguineae* and originally identified and figured by Strasburg (1961: 480) as *C. homei*. The larger specimen possesses a two-chambered swimbladder. Morphometrics (expressed as a ratio to HL; smaller specimen first) of these larvae are as follows: SNL 0.27, 0.24; ED 0.15, 0.15; UJL 0.48, 0.46; LJL 0.52, 0.52; PDL 1.70, 1.77; PAL 1.04; STA 0.96; PL 0.18, 0.23; HW 0.31, 0.32; HD 0.56, 0.57; BD 0.49, 0.54; BI 0.20, 0.16; LTP 1.06, 1.05. Both specimens lack discernible pigment and have damaged jaws preventing reliable dentary description.

Diagnosis.—Primarily (but not exclusively, see Comments) an asteroid-inhabiting species of *Carapus* possessing a free, movable maxilla; a swimbladder with two pseudo-chambers separated by a constriction under vertebrae 9–10; PCV 15–17 and P_1 17–21.

Comments.—Although Arnold (1956) considered Petit's (1934) *Fierasfer mourlani* synonymous with *Encheliophis homei*, Schultz (1960) suggested further study would indicate Petit's type to be distinct. Subsequently, Trott (1970) resurrected *C. mourlani* on the basis of dentition, pigmentation, otolith morphology and host specificity. Our classification places these very similar forms in different genera based on swimbladder morphology. Our examination of additional material generally confirms Trott's (1970) diagnosis with the following qualifications. Conical teeth on the premaxillae in *C. mourlani* tend to be more numerous and more densely packed than those of *En. homei*, but differences are difficult to quantify and are not easily seen without comparative material. Otolith morphology in *C. mourlani* (scalloped vs. smooth in *En. homei*, see Trott, 1970) is variable in our material apparently due to both ontogeny and preservation effects. Pigmentation is also variable, presumably due to length of preservation, but the highly pigmented condition of *C. mourlani* is diagnostic when considering only *E. homei*. Other highly pigmented, similar, sympatric forms are *Encheliophis boraborensis*, *En. vermicularis* and *En. gracilis*. Records of host specificity (Table 6) confirm that

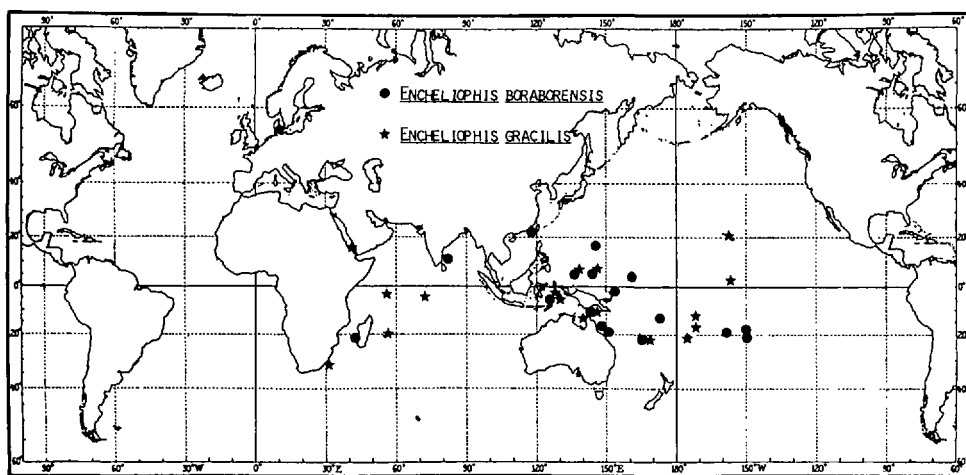


Figure 104. Distribution chart of *Encheliophis boraborensis* and *En. gracilis*.

C. mourlani is a species that primarily inhabits four species of starfishes (Asteroidea); however, 19% of all recorded specimens (Table 6) have been collected in holothurians. Some records of holothurian inquilinism in *C. mourlani* are from localities such as Hawaii, where *En. homei* is not found. However, we found that *C. mourlani* occasionally occupied holothurians around New Caledonia, where *En. homei* is abundant.

Encheliophis Muller

Encheliophis Muller, 1842: 205 (type species, *Encheliophis vermicularis* Muller, 1842: 205, by monotypy).

Jordanicus Gilbert, 1905: 656 (type species, *Fierasfer umbratilis* Jordan and Evermann, 1902: 206, by original designation).

Encheliophiops Reid, 1940: 47 (type species, *Encheliophiops hancocki* Reid, 1940: 47, by original designation).

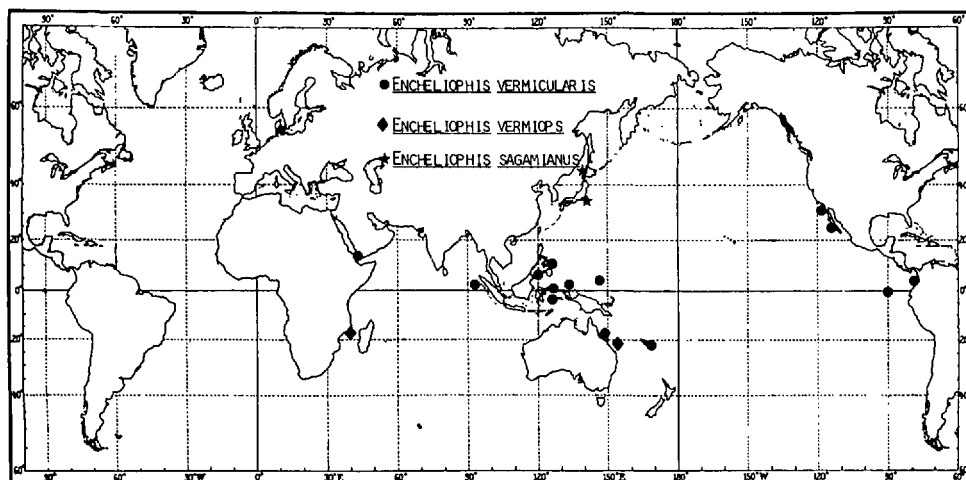


Figure 105. Distribution chart of *Encheliophis vermicularis*, *En. vermiops* new sp., and *En. sagamianus*.

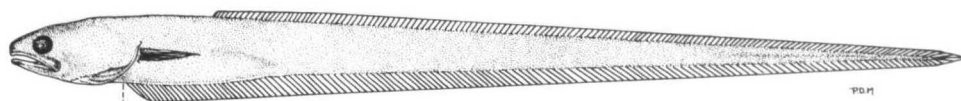


Figure 106. *Encheliophis dubius*, CAS 48987, 14.7 mm HL.

Growth Stages.—Probably three corresponding to vexillifer, tenuis and adult; however, the vexillifer stage is unknown for derived members of the genus.

Diagnosis: Adult.—Carapids lacking pelvic fins, rockerbones, enlarged dentary or premaxillary fangs or diastemae, swimbladder constrictions or tunic ridges and possessing cardiform teeth (probably in all growth stages), a thin, terminal membrane or bulb at the posterior end of the swimbladder (Figs. 32–34), an adnate maxilla (except *En. boraborensis*), fused or partly fused branchiostegal membranes, sometimes reduced pectoral skeleton, no developed gill rakers (except *En. boraborensis*) and obligatory, sometimes parasitic, relationships with species of Holothuria.

Diagnosis: Larvae.—*Carapus*-like larval stages described only for *En. dubius*. More derived species may or may not be similar but probably possess prominent cardiform teeth and a vexillum placement well anterior of the first dorsal-ray (see Ontogeny and Key to Genera sections above).

Comments.—The geographical distribution of *Encheliophis* species is shown in Figures 103, 104, and 105. The depth ranges from about 1 to 110 m.

Encheliophis dubius (Putnam)

Figures 33, 106, Plate 1

Fierasfer caninus Gunther, 1862: 381 (locality unknown), *nomen dubium*.

Fierasfer dubius Putnam, 1874: 339 (Gulf of Panama).

Fierasfer arenicola Jordan and Gilbert, 1881: 338 (off Mazatlan, Mexico).

Fierasfer microdon Gilbert, 1905: 655, fig. 254 (off Hawaii).

Leptofierasfer macrurus Meek and Hildebrand, 1928: 963 (Gulf of Panama).

Synonymy.—We recommend the suppression of Gunther's (1862) name, *F. caninus* (the senior synonym), and the conservation of Putnam's (1874) well established name *dubius*. Putnam was aware of *F. caninus* but Gunther's inadequate description (including lack of type locality or host data) prevented comparison with his material. Gunther's (1862) *F. caninus* could be from any locality worldwide and has caused considerable confusion in the literature; for example, see Smith's (1955a: 403) discussion of *C. mayottae* Smith 1955 and *Jordanicus caninus* Fowler, 1927. Putnam's (1874) name, *F. dubius*, has consistently been applied to the eastern Pacific bivalve inhabitant, but it too requires action in the interest of stability. As noted by Jordan and Evermann (1898) and Arnold (1956), Putnam (1874) had 14 syntypes, six of which are referable to *C. bermudensis* (see that species's account for museum records). His specimens from pearl oysters, Bay of Panama are listed first, and from these we select a lectotype, USNM 153621. The pearl oyster syntypes were deposited at MCZ (MCZ 12421, 2 specimens and MCZ 34037, one specimen). A single specimen from MCZ 34037 was given to USNM (Hartel, in litt., 24 April 1984), but the location of the remaining four syntypes is unknown.

Type Material Examined.—*Fierasfer dubius*, LECTOTYPE, USNM 153621, 10.9 mm HL, F. H. Bradley, Bay of Panama, 1866, from MCZ 34037. *Fierasfer caninus*, HOLOTYPE, BMNH 1952.10.30: 2, 12 mm HL, no data. *Fierasfer arenicola*, HOLOTYPE, USNM 29244, 11.3 mm HL, Mazatlan, Mexico. *Fierasfer microdon*, HOLOTYPE, USNM 51600, 11.5 mm HL, between Maui and Lanai Islds., Hawaii, 16–20 m, from sta. 3872. *Leptofierasfer macrurus*, HOLOTYPE, USNM 82684, 4.0 mm HL, Robert Tweedlie, Chame Pt., Panama.

Other Material Examined: Adult.—16 lots; eastern Pacific localities.

Description: Adults.—Means, ranges and standard deviation of morphometric variables of 14 specimens (8.0–21.9 mm HL, 57–148 mm TL) are as follows,

values expressed as a ratio to HL: SNL 0.19, 0.17–0.23, 0.02; ED 0.22, 0.19–0.26, 0.02; UJL 0.51, 0.46–0.54, 0.02; LJL 0.54, 0.49–0.56, 0.02; PDL 1.65, 1.47–1.85, 0.11; PAL 1.02, 0.95–1.14, 0.06; PL 0.47, 0.41–0.53, 0.03; HW 0.31, 0.26–0.35, 0.03; HD 0.51, 0.43–0.55, 0.04; BD 0.58, 0.51–0.66, 0.06; BI 0.15, 0.14–0.18, 0.01. Average and range of HL as a percent of TL for 14 specimens is 14.8% and 13.7–16.2%. Ranges of meristic variables of 25 specimens are as follows, those of Putnam's cotypes in parenthesis: A_{30} 47–54 (50), D_{30} 35–43 (38), PCV 19–21 (20), VDO 11–13 (12), VAO 3–6 (4), ARDO 17–22 (18), P_1 16–20 (17). The general appearance of *En. dubius* is depicted in Figure 106. Color in preservative is pale brown or tan. External melanophores are sparse and restricted to the snout region, upper and lower jaw and tail tip. In two specimens (CAS 448984), 12–15 silver lateral patches are barely visible, associated with myosepta dorsal to the gut. Internal melanophores are more conspicuous and are primarily concentrated in the brain case dorsal to the brain, along the entire vertebral column, scattered laterally on the abdominal wall and dorsal to the swimbladder.

The teeth on premaxilla are small, conical, somewhat recurved and polyserial. Two to four larger conical teeth are at the tip of the premaxilla. An outer row of recurved cardiform teeth occupies the anterior third of the premaxilla. The dentary has an outer row of conical teeth, those of the anterior jaw stout and large and not tightly spaced, gradually becoming smaller posteriorly. Inner dentary teeth are short, blunt and polyserial. The palatine is covered with densely packed, polyserial, blunt teeth. The vomer has five to seven large, stout, median fangs which are flanked by small, blunt, polyserial teeth. Except for the number of median vomerine fangs, the tooth pattern described above is not exceptionally variable in the size range examined.

There are no lateral line scales, teeth are present on hypobranchial 3 and the swimbladder lacks intrinsic constrictions (Fig. 33).

Description: Larvae.—In addition to the type of *Leptofierasfer macrurus* (Meek and Hildebrand, 1928), first recognized by Parr (1930) as a larva, we have examined one vexillifer (SIO 63-952, 3.5 mm HL) and one tenuis larva (ZMUC CN3, 4.8 mm HL) of *En. dubius*. Identifications of these two specimens are based primarily on distributional records although meristic variability enables separation from its sympatric congener, *En. vermicularis*. The vexillifer larva (SIO 63-952) was originally illustrated and described by Trott (1970: 19, pl. 11B) as *Encheliophis jordani* based on an adnate maxilla and no pectoral fins. The specimen is somewhat damaged, likely contributing to these erroneous observations, does not have an adnate maxilla and has pectoral fins. We record the following counts from the specimen which we have cleared and stained: P_1 20+, A_{30} 52, D_{30} 37, VVO 4, VDO 12, VAO 6, PCV 19, ARDO 18. Selected morphometric variables expressed as a ratio to HL are as follows: SNL 0.18; ED 0.21; LJL 0.54; PVL 1.24; PAL 1.44; STA 1.21; HD 0.73; BD 0.48. A prominent, single cardiform tooth is visible at the tip of the premaxilla. The specimen is similar in general appearance to Figure 94. The morphology and position of the modified radial supporting the vexillum is as described for *C. bermudensis* (Olney and Markle, 1979). The tenuis larva (ZMUC CN3, 4.8 mm HL) is contorted (about 70 mm TL) and discolored. Counts recorded are ARDO 19 and MDO 12–13. A single prominent cardiform tooth is visible on the premaxilla and small, sharp conical teeth are visible on the dentary and palatine. The vomer appears toothless.

Diagnosis.—A molluscan-inhabiting species of *Encheliophis* possessing a free, movable maxilla, a swimbladder without pseudo-chambers, PCV 19–21 and A_{30} 47–54.

Comments.—*Encheliophis dubius* may be the only species of the genus which is an obligate molluscan inquiline (Table 6). We examined a particularly striking example (Pl. 1) of this host relationship (MCZ 72903, Mollusk Dept.) in which an adult *En. dubius* (about 10.0 mm HL) is encased as a blister pearl in the valve of *Pinctada mazatlanica* (identification of host confirmed by K. Boss, pers. comm., 24 April 1984). This may be the same specimen examined by Putnam (1874). Such a bizarre fate may not be unusual since at least three additional specimens, presumably *En. dubius*, have been found "entombed in nacreous splendor" (Gunter, 1886; Stearns, 1887; Nelson, 1928).

Populations of *En. dubius* may be widespread. Confirmed records are in the eastern Pacific from the Gulf of California to Colombia and from Hawaii (*F. microdon* Gilbert, 1905). The report of Trott and Chan (1972) of *En. homei* in *Tridacna* may refer to *En. dubius* in the South China Sea. Our extensive efforts to locate this specimen have been unsuccessful and the specimen may be lost (P. Mak and K. C. Au, pers. comm., 3 Dec. 1984).

Encheliophis homei (Richardson)

Figures 1, 6, 33, 107

Oxybeles homei Richardson, 1844: 73 (questionably, Tasmania or Timor I.).

Type Material Examined.—*Oxybeles homei*, HOLOTYPE, BMNH 1952.10.30:3, 14.8 mm HL (measurement taken from radiograph), Sir James Ross, locality unknown but probably Tasmania (Richardson, 1844: 73). *Fierasfer affinis*, HOLOTYPE, BMNH 1952.10.30:1, 20.5 mm HL (measurement taken from radiograph), locality unknown.

Other Material Examined: Adult.—64 lots; Pacific and Indian Oceans.

Description: Adult.—Mean, range and standard deviation of morphometric variables in 13 specimens (10.2–26.0 mm HL, 76–190 mm TL) are as follows, values expressed as a ratio to HL: SNL 0.13, 0.13–0.20, 0.02; ED 0.21, 0.16–0.28, 0.04; UJL 0.48, 0.45–0.51, 0.02; LJL 0.51, 0.48–0.53, 0.01; PDL 1.77, 1.62–1.88, 0.09; PAL 0.91, 0.86–0.97, 0.03; PL 0.45, 0.39–0.53, 0.05; HW 0.36, 0.30–0.42, 0.03; HD 0.48, 0.43–0.53, 0.03; BD 0.57, 0.46–0.69, 0.06; BI 0.16, 0.12–0.18, 0.02. The range of meristic variables of 36 specimens are as follows, those of the holotype in parentheses (the radiograph of the specimen is poor and does not allow full meristic analysis): P₁ 17–21, A₃₀ 53–61 (57), D₃₀ 33–38, PCV 16–19 (17), VDO 12–14, VAO 1–4 (3), ARDO 19–26. The general appearance of *Encheliophis homei* is illustrated in Figure 107. Color in preservative is pale to tan. In freshly preserved material, a series of at least ten silvery patches is visible associated with abdominal myotome segments. Externally the body is generally without pigment with the exception of large stellate melanophores along the tip of the snout and the lower jaw. These stellate melanophores are hidden by the adductor mandibulae. Internal pigmentation is conspicuous over the brain (somewhat silvery in fresh material, see Trott, 1981 for notes on live coloration around the head), in the epaxial musculature behind the brain case, and associated with the vertebral column. The peritoneum is silvery with densely scattered melanophores, giving the entire abdominal region a dark appearance. In addition, the nasal rosette is darkly pigmented.

The anterior half of the premaxilla has an outer row of 13–15 cardiform teeth that increase in size anteriorly. The inner premaxillary teeth are conical and in two rows, the teeth of the inner row curving inward. One large, stout conical tooth is at the tip of the premaxilla. Conical teeth of the dentary are larger and less tightly spaced than premaxillary teeth and in a single row. At the tip of the dentary, the single row grades into a short double row, the outer teeth being smaller. Inner

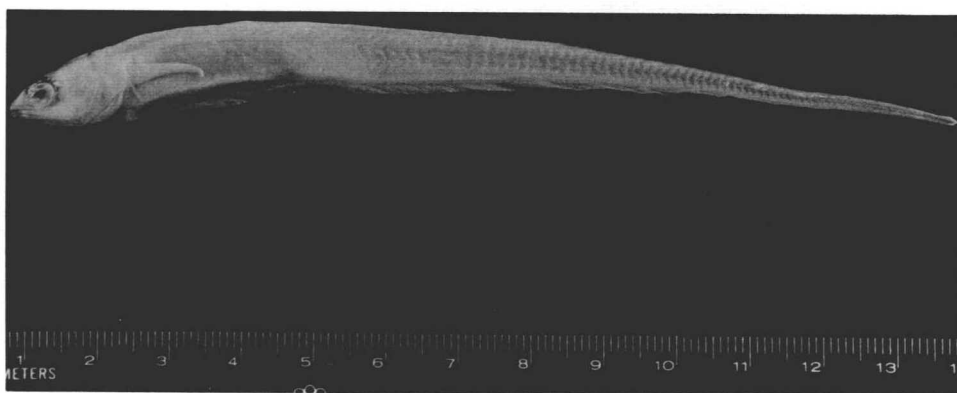


Figure 107. *Encheliophis homei*, OS 12482, 18.7 mm HL.

dentary teeth are very short, blunt and polyserial. The vomer bears 3–6 large, stout conical teeth (one median tooth is usually largest) flanked by smaller, blunt teeth. Palatine teeth are small, conical and polyserial (although tending to be organized in three rows).

Neural and haemal spines are spatulate.

Description: Larvae. — Vexillifer and tenuis larvae of *En. homei* are unknown (see genus account).

Diagnosis. — A holothurian-inhabiting (perhaps exclusively) species of *Encheliophis* possessing a free, movable maxilla, a swimbladder without an intrinsic constriction, PCV 16–19 and A_{30} 53–61.

Comments. — *Encheliophis homei* is most similar to *En. dubius* but differs in distribution, precaudal vertebral counts, anal fin-ray counts, and host preference. Arnold (1956) regarded Gilbert's (1905) *F. microdon* as a junior synonym of *En. homei* and thus included Hawaii in its distribution range. Our examination of type material (see *En. dubius* account, Fig. 108) leads us to a different conclusion. *Encheliophis homei* occurs as far north as Taiwan (TFRI no. 885, 25.5 mm HL) but apparently is not found in Hawaii.

Encheliophis boraborensis (Kaup)

Figures 12, 32, 109

Fierasfer boraborensis Kaup, 1856: 99 (Bora Bora I.).

Fierasfer parvipinnis Kaup, 1856: 99 (Papua New Guinea).

Rhizoiketicus carolinensis Vaillant, 1893.

Synonymy. — Kaup's (1856) brief description of *F. boraborensis* appears before that of *F. parvipinnis*. His decision not to consider these two forms as conspecific is inexplicable. We have not examined the type of *F. kagoshimianus* Steindachner and Doderlein (1887) which neither we nor Arnold (1956) could locate and which may also be a junior synonym of *E. boraborensis*.

Type Material Examined. — *Fierasfer boraborensis*, HOLOTYPE, MNHN B1265, 29.0 mm HL (measurement from radiograph), Lesson and Garnot, Bora Bora I., Society Is. *Fierasfer parvipinnis* MNHN B1264, COTYPES, three specimens, 20.0, 20.0, 27.5 mm HL (measurements from radiographs), Quoy and Gaimard, Carteret Harbor, New Ireland I., Papua New Guinea. *Rhizoiketicus carolinensis*, COTYPES, MNHN 1889-9 and 10, 20.5 and 24.5 mm HL (measurements from radiograph).

Other Material Examined: Adult. — 70 lots; Pacific and Indian Oceans.

Description: Adult. — Means, ranges and standard deviation in morphometrics of

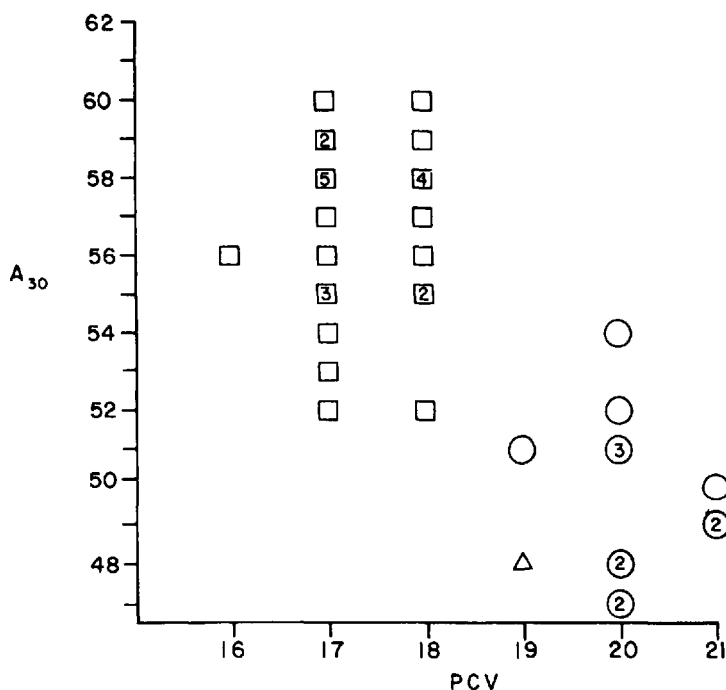


Figure 108. Comparison of selected meristic characters of *Encheliophis dubius* (circles), *En. homei* (squares), and the holotype of *Fierasfer microdon* (triangle); numerals within symbols indicate multiple observations.

nine specimens (11.4–33.5 mm HL, 100–334 mm TL) are as follows, values expressed as a ratio to HL: SNL 0.17, 0.13–0.24, 0.03; ED 0.13, 0.11–0.15, 0.03; UJL 0.51, 0.42–0.53, 0.03; LJL 0.51, 0.45–0.54, 0.03; PDL 1.91, 1.77–2.15, 0.14; PAL 1.08, 0.95–1.37, 0.13; PL 0.24, 0.20–0.28, 0.03; HW 0.50, 0.38–0.68, 0.09; HD 0.55, 0.51–0.58, 0.03; BD 0.65, 0.57–0.81, 0.07; BI 0.19, 0.14–0.24, 0.03. Meristic values recorded from Kaup's holotype (MNHN B1265) are: A₃₀ 50, D₃₀ 36, PCV 17, VDO 13, VAO 5, ARDO 17. The general appearance of *Encheliophis boraborensis* is illustrated in Figure 109. Color in life is deep reddish brown over the entire body including fins (Trott, 1970; Masuda et al., 1984: pl. 84C; J. Randall color photograph). Color in preservative is pale to dark brown. The entire body is covered with uniformly scattered, small, stellate melanophores.

The anterior half of premaxilla bears an outer row of 11–13 cardiform teeth, the largest at the jaw tip and gradually decreasing in size posteriorly. The remaining premaxillary teeth are conical and polyserial, in more or less three rows with the teeth of the inner row largest. The dentary has an outer, polyserial patch of small conical teeth situated on the anterior third of the toothed portion of the jaw. An inner median row of larger conical teeth is polyserial anteriorly, becoming a single row posteriorly. Inner dentary teeth short, conical, polyserial. Teeth on the palatine are short, stout, conical and polyserial. The median series is larger than inner or outer series. The vomerine teeth are short, stout and conical. Median teeth are larger (especially in smaller specimens) than those of the fringing series.

There is no predorsal bone. Lateral line scales are present. Pelvic bones present with cartilaginous distal tip. Swimbladder lacks intrinsic constrictions (Fig. 32).

Description: Larvae.—Vexillifer and tenuis larvae of *Encheliophis boraborensis*

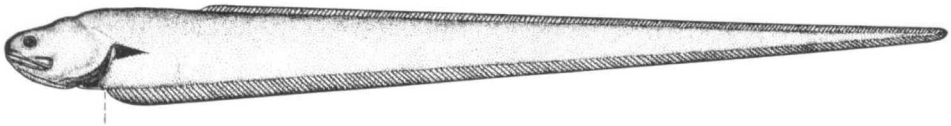


Figure 109. *Encheliophis boraborensis*, OS 12483, 23.5 mm HL.

are undescribed, but specimens ranging from 5.9–10.0 mm HL and 50–80 mm TL possess pre-metamorphic pigment. Meristic and morphometric values are within those ranges given for adults except values for PL which ranged from 0.07–0.10 (ratio to HL). Color in alcohol is pale. In the smallest specimens, small, stellate melanophores are visible at the tip of the jaws, associated with the nasal rosette, on the posterior brain and widely scattered along the flank, posterior to the pectoral fin. The rest of the body, including fins, is unpigmented. Melanophores gradually increase in number with increasing HL, approaching the adult condition. Two cleared and stained specimens (OS 12481, 5.8, 6.2 mm HL; 51, 57 mm TL) lack lateral line scales (present in adults) and possess an accessory cartilage anterior to the second neural spine (absent in adults). In addition, a bean-shaped cartilage, presumably the distal radial of the vexillar support, is visible over the fourth centrum.

Diagnosis.—A holothurian-inhabiting species of *Encheliophis* that has a free, movable maxilla, a swimbladder without pseudo-chambers, a small eye, a short pectoral fin and PCV 15–17.

Comments.—This is the largest species of *Encheliophis* and, not surprisingly, appears to prefer one of the largest holothurians, *Thelenota ananas*.

Encheliophis gracilis (Bleeker)
Figures 6, 12, 20, 26, 27, 33, 110

Oxebeles gracilis Bleeker, 1856: 105 (Banda I.).

Fierasfer umbratilis Jordan and Evermann, 1902: 206 (Hawaii).

Fierasfer houlti Ogilby, 1922: 301 (Australia).

Type Material Examined.—*Oxebeles gracilis*, HOLOTYPE, BMNH 1961.2.28:51, 12.0 mm HL (measurement from radiograph), Bleeker Collection, Banda. *Fierasfer houlti*, HOLOTYPE, QM I3444, 36.3 mm HL, 275 mm TL, Capt. Houlty, Trawler Bar-ea-Mul, off Double Island Point, S.E.W., 36 fm., in eviscerated holothurian. *Fierasfer umbratilis*, HOLOTYPE, USNM 50656, 19.0 mm HL (measurement from radiograph), Jordan and Evermann, Hilo, Hawaii. *Fierasfer umbratilis*, COTYPE, CAS (SU) 7470, 14.5 mm HL, Jordan and Evermann, Hilo, Hawaii (Jordan and Evermann, 1903: 505–506, pl. 61 state that their material of *F. umbratilis* was designated (by monotypy) as the type of *Jordanicus* Gilbert, 1905 and figured a specimen, presumably their field no. 03506).

Other Material Examined: Adult.—81 lots; Pacific and Indian Oceans.

Description: Adult.—Means, ranges and standard deviation of morphometric variables of 10 specimens (5.8–36.3 mm HL, 89–275 mm TL) are as follows, values expressed as a ratio to HL: SNL 0.17, 0.14–0.21, 0.02; ED 0.20, 0.19–0.23, 0.02; UJL 0.39, 0.34–0.48, 0.04; LJL 0.48, 0.39–0.61, 0.06; PDL 2.07, 1.84–2.38, 0.17; PAL 1.05, 0.99–1.12, 0.05; STA 0.96, 0.90–1.07, 0.05; PL 0.25, 0.15–0.32, 0.06;

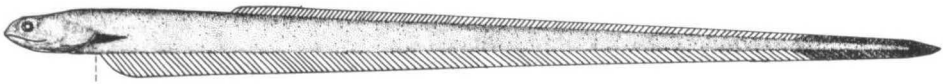


Figure 110. *Encheliophis gracilis*, OS 12484, 21.0 mm HL.

Table 19. Morphometric comparison for available specimens of *Encheliophis sagamianus* (All values except HL and TL are expressed as a ratio to HL)

	MCZ 30750				AMNH 13034
HL (mm)	10	18.3	18.4	20.4	15.3
TL (mm)	100	180	186	200	152
SNL	0.2	0.2	0.2	0.2	0.2
ED	0.3	0.2	0.2	0.2	0.2
UJL	0.4	0.5	0.5	0.4	0.5
LJL	0.5	0.6	0.5	0.6	0.6
PDL	—	1.8	1.9	1.8	—
PAL	1.2	1.2	1.1	0.9	1.1
STA	0.9	1.0	0.9	0.9	1.0
PL	0.2	0.2	0.2	0.3	0.3
HW	0.3	0.4	0.4	0.4	0.4
HD	0.5	0.5	0.5	0.5	0.5
BD	0.6	0.7	0.7	0.7	0.75
BI	0.2	0.2	0.2	0.2	0.2
LTP	1.0	0.9	1.0	0.9	1.0

HW 0.34, 0.28–0.39, 0.04; HD 0.38, 0.34–0.43, 0.03. Meristic values are as follows, those of Bleeker's (1856) holotype in parentheses: P₁ 17–19, A₃₀ 42–52 (49), D₃₀ 25–36 (36), VDO 13–17 (13), VAO 3–6 (5), PCV 26–32 (29), ARDO 19–27 (19). The general appearance of *En. gracilis* is depicted in Figure 110 (also see color plate of Jordan and Evermann, 1903: pl. 61). Masuda et al. (1984) illustrate a fresh specimen, and Trott (1970) provides notes on living coloration. As noted by Arnold (1956) Jordan and Evermann's (1902: 206) description of live pigmentation must be in error considering the reference to ventral fin coloration. Color in preservative is tan to brown. Melanophores are scattered evenly around the body but densely distributed on the head, gill cover and branchiostegal membrane. The posterior portions of the dorsal and anal fins are jet black. The remaining portions of dorsal, anal and pectoral fins are largely unpigmented and the lateral line is distinct.

The maxilla is partly adnate and toothless. The premaxilla bears a single row of recurved cardiform teeth (Fig. 27). Both dentary and palatines have a single row of conical teeth, those of the dentary larger. The vomer has 3–4 stout, recurved fangs, the posterior teeth usually largest.

An accessory cartilage is above the 4th neural spine. Caudal neural and haemal spines are spatulate. The swimbladder is pigmented, has a sclerified anterior portion and lacks intrinsic constrictions (Fig. 33).

Description: Larvae.—The larva of *En. gracilis* is unknown. A single tenuis larva (5.8 mm HL, 89 mm TL) possesses premetamorphic pigment consisting of large stellate melanophores scattered on top of the head, the snout tip, upper and lower jaws and the gill cover. A patch of 10–12 melanophores is visible just posterior to the pectoral fin along the gut. In addition, lateral melanophores associated with myosepta begin at myomere 23–25 and extend to the tail, increasing in density posteriorly. Overall, the preserved specimen is pale. With development, lateral melanophores become more dense and the body darkens in lateral aspect. Epaxial musculature above the gut is the last lateral area to become covered with melanophores.

At 5.8 mm HL, the premaxilla possesses a single cardiform tooth at the jaw tip followed by a single row of smaller, slender conical teeth. With development,



Figure 111. *Encheliophis sagamianus*, MCZ 30750, 18.4 mm HL.

cardiform teeth increase in number (e.g., $N = 2$ at 5.6 mm HL; $N = 8$ at 6.4 mm HL) forming on the outside of a short row of conical teeth. This inner tooth row is not visible in an 8.3 mm HL juvenile and is absent in adults.

Diagnosis.—A holothurian-inhabiting species of *Encheliophis* possessing an adnate maxilla, P_1 17–19; A_{30} 42–52 and PCV 26–32.

Encheliophis sagamianus (Tanaka)

Figures 23, 34, 111

Carapus sagamianus Tanaka, 1908: 40 (Sagami Bay, Japan).

Type Material Examined.—*Carapus sagamianus*, radiograph of HOLOTYPE, ZUMT 1751, 16.1 mm HL, Sagami Sea, Mr. Aoki, 1908. *Carapus sagamianus*, radiograph of PARATYPES, ZUMT 1752, eight specimens, 10.0–14.2 mm HL, same collection data as holotype.

Material Examined.—AMNH 13034, 15.3 mm HL, 152 mm TL, Otaru, Japan, 4 IX 1922. MCZ 30750, 4 specimens (one cleared and stained), 10.0–20.4 mm HL, 100–200 mm TL, Owston Collection 9253, Sagami Sea, Japan, Dec. 1906.

Description: Adults.—Morphometric variables are summarized in Table 19. Ranges of meristic variables of 11 specimens, those of the holotype in parentheses, are as follows: P_1 15–16, A_{30} 39–45 (45), D_{30} 28–35 (35), PCV 20–24 (20), VDO 11–14 (11), VAO 3–5 (4), ARDO 12–18 (14). The general appearance of *En. sagamianus* is illustrated in Figure 111. Color in preservative is tan to brown and melanophores are evident only on the smallest specimen at hand (MCZ 30750, 10.0 mm HL), scattered around the anus and the branchiostegal rays and somewhat concentrated along dorsal- and anal-fin bases on the posterior third of the body. Tanaka's (1908) notes and illustration [Masuda et al., 1984: 99 reproduced Tanaka's (1951) drawing] indicate that freshly preserved specimens are more profusely pigmented than our material suggests.

The maxilla is adnate and toothless. Premaxillae bear a single outer row of recurved cardiform teeth and an inner row of small conical teeth. The dentary has a single row of conical teeth. Those of the palatine are polyserial and alternating in direction. The vomer is covered with a dense patch of small blunt teeth. Vomerine dentition may vary since we note Tanaka's (1908) description is not in agreement with our observations of MCZ 30750.

An accessory cartilage is present and haemal spines are spatulate. A series of dorsal radials without fin rays precedes the first dorsal-fin ray.

Table 20. Morphometric comparison of known specimens of *Encheliophis vermiops* (All values except HL and TL are expressed as a ratio to HL)

	Holotype	Paratype	RUSI#12196
HL (mm)	7.1	9.2	4.8
TL (mm)	97	138	62
SNL	0.2	0.1	0.2
ED	0.2	0.2	0.2
UJL	0.3	0.3	0.3
LJL	0.4	0.4	0.5
PDL	3.3	—	—
PAL	1.3	1.3	1.1
STA	1.1	1.1	1.1
PL	0.4	0.4	0.3
HW	0.4	0.6	0.3
HD	0.5	0.6	0.4
BD	0.5	0.8	0.4
BI	0.2	0.2	0.1
LTP	1.1	1.1	1.1

Description: Larvae.—The larval stages of *En. sagamianus* are unknown; illustrations in Okiyama (1986) are of *Echiodon* unnamed (27.5 mm TL) and *coheni* (77.0 mm TL).

Diagnosis.—A holothurian-inhabiting species of *Encheliophis* with an adnate maxillary, PCV 20–24, P₁ 15–16, ARDO 12–18 and VDO 11–14. The species is known only from Japan.

Comments.—Natural history data are sparse. Tanaka (1908) reports the species is often taken in larger holothurians. Masuda et al. (1984) consider the species to be a deep water form distributed northward to the Sagaminada Sea and Toyama Bay. We have not been able to confirm several unreferenced host records listed by Arnold (1956: 302) for this species.

After this manuscript was accepted we received four IOAN specimens of *Encheliophis* collected at 11°21'06"S, 61°46'08"E, 87–110 m, on 7 January 1989. The specimens generally agree with our description of *E. sagamianus* but have fewer precaudal vertebrae (19–20), are small (77–102 mm TL) and ripe. Thus, they appear to represent another dwarf species, such as *E. vermiops*.

Encheliophis vermiops new species

Figures 34, 112

Type Material Examined.—*Encheliophis vermiops*, HOLOTYPE, AMS IB.5245, 7.1 mm HL, 97 mm TL, female (?), J. Bishop, Heron Isld., Queensland, Australia, Sandbank towards wreck, 18 I 1961, inside of burrowing holothurian. *Encheliophis vermiops*, PARATYPE, AMS IB.5244, 9.2 mm HL, 138 mm TL, J. Bishop, Heron Isld., Queensland, Australia, I 1961.

Other Material Examined: Adult.—RUSI 12196, 4.8 mm HL, 62 mm TL, Zoology Dept., Univ. of Witwatersrand, North Bay, Inhaca, South Africa, Sept. 1958.

Description of Type Material.—A morphometric comparison of type and non-type material is presented in Table 20. Measurements of the holotype (mm) are: SNL 1.0; ED 1.2; UJL 2.3; LJL 2.7; PDL 23.5; PAL 9.5; STA 8.0; PL 2.9; HW 3.1; HD 3.4; BD 3.5; BI 1.1; LTP 7.7. Head length as a percent of total length in type and non-type material ranged from 6.7–7.8%.

Meristic values of type material are as follows: A₃₀ 40; D₃₀ 28; PCV 22; VDO

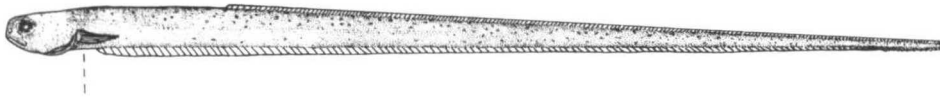


Figure 112. *Encheliophis vermiops*, holotype, AMS 5245, 7.1 mm HL.

16; VAO 5; ARDO 19–20; P₁ 15–16. Pectoral-fin ray and precaudal vertebral counts of RUSI 12196 are 15 and 20, respectively. No other meristic values were available for this specimen.

The general appearance of the holotype of *En. vermiops* is illustrated in Figure 112. The overall color in ethanol is tan with head and body pigmentation consisting of relatively large, stellate melanophores widely scattered over every aspect of the body. The dorsum and posterior tip of the tail are more heavily pigmented than the ventral aspect. The abdominal wall is covered with very large stellate melanophores. Dorsal-, anal- and pectoral-fin rays are unpigmented except for the extreme posterior dorsal- and anal-fin bases. A caudal fin is not visible. Pigment on the larger paratype is similarly distributed; however, this specimen is darker.

The posterior portion of the maxilla is partly adnate. Cardiform teeth are present on the premaxilla. Enlarged fangs are absent. The dentary and palatine bear tightly spaced triangular teeth that appear to interdigitate. The swimbladder is short and without pseudo-chambers (Fig. 34B).

Description: Larvae.—Vexillifer and tenuis larvae are unknown.

Diagnosis.—A holothurian-inhabiting, diminutive species of *Encheliophis* with an adnate maxilla, PCV 20–22, P₁ 15–16, ARDO 19–20 and VDO 16. The species is known only from the southern hemisphere.

Comments.—Natural history data are sparse. The species, known only from two adults (Heron Island, Australia) and a juvenile (Inhaca, South Africa), apparently is an inquiline in an unknown species of burrowing holothurian. Attempts by colleagues to identify the host and collect additional material have been unsuccessful. The species is most closely related to *En. gracilis* and *En. sagamianus*. All have high precaudal vertebral counts, partly adnate maxillae and 15–19 pectoral rays. Both *En. vermiops* and *En. sagamianus* possess small swimbladders (Fig. 34).

Table 21. Comparison of selected morphometrics in three widely distributed populations of *Encheliophis vermicularis* (All values except HL and TL are expressed as a ratio to HL)

	Eastern Pacific			Western Pacific			Gulf of Aden		
	N	Range	\bar{x}	N	Range	\bar{x}	N	Range	\bar{x}
HL (mm)	6	6.1–11.4	8.4	5	6.2–13.0	9.3	3	9.0–13.5	11.7
TL (mm)	6	71–118	100	5	69–132	99	3	80–124	98
SNL	6	0.2–0.2	0.2	5	0.2–0.2	0.2	3	0.2–0.2	0.2
ED	6	0.1–0.2	0.1	5	0.1–0.2	0.1	3	0.1–0.2	0.1
LJL	6	0.5–0.6	0.5	5	0.5–0.6	0.5	3	0.5–0.6	0.5
PDL	4	2.2–2.5	2.4	3	2.3–2.6	2.5	3	2.1–2.5	2.4
PAL	6	1.1–1.3	1.2	4	1.1–1.2	1.1	3	1.0–1.2	1.1
STA	6	0.9–1.1	1.1	5	0.9–1.1	1.0	3	0.9–1.1	1.0
HD	6	0.4–0.4	0.4	5	0.3–0.5	0.4	3	0.4–0.5	0.5
BD	6	0.4–0.6	0.5	4	0.3–0.6	0.5	3	0.5–0.7	0.6

Table 22. Comparison of selected meristics in three widely distributed populations of *Encheliophis vermicularis*

	Eastern Pacific			Western Pacific			Gulf of Aden		
	N	Range	\bar{x}	N	Range	\bar{x}	N	Range	\bar{x}
A ₃₀	10	38–43	40.5	17	36–43	40.5	3	37–41	39.7
D ₃₀	10	21–26	24.8	18	21–27	24.8	3	19–26	22.7
PCV	10	20–23	21.3	19	20–22	21.3	3	20–21	20.3
VDO	10	16–17	17.2	18	16–19	16.6	3	16–19	17.0
VAO	10	5–6	5.5	18	4–6	5.5	3	4–5	4.3
ARDO	10	17–22	19.4	17	17–24	19.4	3	17–23	19.7

Etymology.—In reference to the general appearance of the head, a combination of the Latin “vermis” meaning worm and the Greek “ops” meaning “face,” to be treated as an appositional noun.

Encheliophis vermicularis Muller
Figures 34, 113

Encheliophis vermicularis Muller, 1842: 205 (Philippine Is.).

Encheliophis jordani Heller and Snodgrass, 1903: 220 (Galapagos Is.).

Encheliophis hancocki Reid, 1940: 47 (off Colombia).

Synonymy and Neotype Description.—Muller's (1842) type of *Encheliophis vermicularis* (type locality Philippines) could not be located in European museums. Most of Muller's material was incorporated into the Museum für Naturkunde der Humboldt-Universität zu Berlin, but not all was kept according to H. J. Paepke (pers. comm., 1 June 1984). At our request, H. J. Paepke attempted to locate Muller's specimen but could find no carapide type material in ZMB. We, therefore, consider Muller's holotype lost and designate the neotype described below. The type locality and additional specimens that were collected with the neotype are described by Murdy and Cowan (1980).

Type Material Examined.—*Encheliophis vermicularis*, NEOTYPE, USNM 298307, 12.8 mm HL, 130 mm TL, gravid female, M. E. Cowan, Samar Sea Coll., Calatagan Lagoon, Batangas, Philippine Is., 13°49'N, 120°37'E, 0–1 m, 8 March 1980, one of six specimens removed from *Holothuria scabra*. *Encheliophis jordani*, HOLOTYPE, CAS (SU) 6345, 10.0 mm HL, Tagus Cove, Albemarle Isld., Galapagos Is., 1898 or 1899.

Other Material Examined: Adult.—31 lots; Eastern Pacific, Indo-west Pacific and Gulf of Aden.

Description: Adults.—Summaries of morphometric and meristic data are presented in Tables 21 and 22. Measurements (mm) for the neotype are as follows: SNL 2.3; ED 1.9; L JL 6.7; PDL 30.0; PAL 14.9; STA 13.9; HW 5.1; HD 6.6; BD 8.0; BI 2.5. Meristic values of the neotype are: A₃₀ 38, D₃₀ 22, PCV 21, VDO 17, VAO 6, ARDO 19.

Encheliophis vermicularis is illustrated in Figure 113. In preserved material body color is generally tan. Melanophores are concentrated at the tip of the snout, the tip of the tail and along the lateral midline. In large specimens, lateral pigment in the form of large stellate melanophores extends from just anterior of the body mid-point to the caudal tip. Anteriorly, these melanophores are scattered above and below the mid-line, becoming dark and more dense posteriorly. The posterior tenth of the body is jet black in most specimens with pigment extending to the edges of both dorsal and anal fins. In addition, internal melanophores associated with myosepta form in series along the mid-line. Internal stellate melanophores are also visible scattered over the peritoneum and in dense concentrations on the dorsal abdominal wall. This pigment pattern is most easily seen in large females with distended guts. In smaller specimens peritoneal pigment is inconspicuous. In the head region of large adults, melanophores are distributed on the upper and

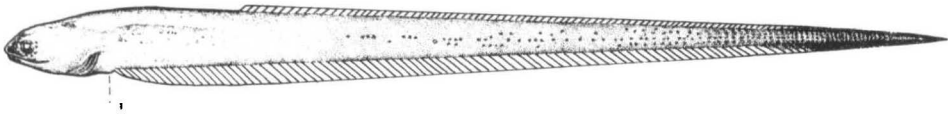


Figure 113. *Encheliophis vermicularis*, OS 12485, 14.0 mm HL.

lower jaws and in a ventral series around the orbit. The cheek is largely unpigmented.

In our material, variability in the pigment patterns described above results largely from length of preservation and ontogeny. We did not find sexually dimorphic pigment in preserved material nor did Murdy and Cowan (1980) in examination of living specimens. Masuda et al. (1984) illustrate apparent pigment dimorphism in fresh material but without comment. In our re-examination of Murdy and Cowan's (1980) specimens (now preserved in ethanol), we did not observe the conspicuous blue pigment noted by these authors.

The maxilla is adnate and toothless. The premaxilla bears an outer row of recurved cardiform teeth and an inner row of conical teeth. The dentary and palatine have a single row of conical teeth, those on the dentary longer than those of the premaxilla or palatine. The vomer bears 6–7 conical, somewhat recurved teeth, usually spaced in groups of three anterior and three posterior.

The first neural spine is ankylosed to the skull and neural spines 2, 3 and 4 are very broad in lateral view. The anterior lateral line pores react positively to stain. Haemal spines are spatulate. There is no predorsal bone. The swimbladder is long and lacks intrinsic constrictions (Fig. 34).

Description: Larvae.—Larvae of *En. vermicularis* could not be identified (see discussion under genus). The larval specimen identified and illustrated by Trott (1970) as *Encheliophis jordani* (SIO 63-952) has been cleared and stained and re-identified as *En. dubius* (see *En. dubius* account).

Diagnosis.—A holothurian-inhabiting species of *Encheliophis* which lacks an externally visible pectoral fin, and possesses an adnate maxillary and D_{30} 19–27.

Comments.—Collection records are bounded by 30°N and 30°S latitudes (Fig. 105). *Encheliophis vermicularis* is widely distributed within the Indo-Pacific region from New Caledonia to the Adaman Sea. In addition to numerous specimens from the Gulf of California and Galapagos Is., *En. vermicularis* has been collected in the Red Sea.

We recognize one wide-ranging species of *En. vermicularis* with three seemingly isolated populations: The Gulf of Aden, Indo-west Pacific and the eastern Pacific. Although eastern Pacific material tends to be smaller in TL and have a smaller eye and head (Table 21), we observed complete overlap in all morphometric and meristic characters (Tables 21, 22). Pigmentation characters used in separation of eastern and western Pacific populations by Reid (1940) are invalid and differences in live colors are currently unexplained but possibly sexual (Masuda et al., 1984). We noticed several traits which appeared to show east-west clinal variation. In meristic characters, A_{30} , D_{30} , PCV and VAO had low mean values in the Gulf of Aden, and higher values in the western Pacific and Gulf of California. In addition, HL/TL tended to be highest in the Gulf of Aden and lowest in the eastern Pacific. A decision to assign subspecific rank to these populations is deferred until additional material, including larval forms, is encountered.

Natural history data on *En. vermicularis* are limited to records of male/female

pairing and host parasitism by Murdy and Cowan (1980). Identifications of known *En. vermicularis* hosts are summarized in Table 6.

ZOOGEOGRAPHY

The only previous discussion of carapid zoogeography was by Springer (1982) in his review of zoogeography of Pacific Plate shorefishes. He noted that six species had been taken non-marginally on the Plate and that there were fewer than 10 Indo-Pacific carapids. We concur that there are records of adults of only six carapine species, but note the presence also of *P. ventralis* and *S. canina*, the possible presence of *P. parini*, the presence of larvae of *O. parvibrachium* and *Echiodon* unnamed, as well as Trott's recent collection of adult *O. parvibrachium* from Hawaii (see species account). We would also revise the total number of Indo-Pacific carapid species to 26 (including the eastern Pacific *Ec. exsilium*). Springer (1982) was concerned with shorefishes and our revised total of Indo-Pacific carapids includes outer shelf and continental slope species as well. However, the revised maximum estimate of 11 Pacific Plate species out of 26 Indo-Pacific carapids gives a percentage representation on the Plate (42%) close to the average (33%) and within the limits (20–50%) that Springer (1982: 120) reports for well-known, speciose families.

Pyramodontinae.—*Pyramodon* and *Snyderidia* distributions are broadly overlapping in the Indian Ocean and central and western Pacific (Fig. 48). They are allopatric in the Atlantic (*S. canina* only) and eastern South Pacific (*P. parini*). A simple scenario would call for vicariance of an ancestral Atlantic-Pacific pyramodontine, followed by relatively recent dispersal of the Atlantic form (*Snyderidia*) into the Indo-Pacific. A recent dispersal event or an unidentified capacity to maintain gene flow is necessary in order to account for the distributional pattern and lack of differentiation of Atlantic and Indo-Pacific *S. canina*. *Snyderidia canina* has the broadest longitudinal distribution of any carapid (Fig. 48).

An unresolved trichotomy in our *Pyramodon* cladogram (Fig. 44) obviously restricts our discussion of *Pyramodon* zoogeography. We note, however, that all four species are allopatric (Figs. 48, 114). Considering that our cladogram specifies that *P. parini* must be part of a larger track with *P. ventralis*, then *P. punctatus* is the geographically most isolated species with a distribution center around 40°S (Fig. 114). It also has the greatest depth range (120–731 m compared to 184–385 m for all other *Pyramodon*). An early event in *Pyramodon* evolution might have involved isolation of this relatively deeper, southern form from a relatively shallow, northern form. The evidence implicates bathymetric as well as latitudinal events in *Pyramodon* evolution, but does not help resolve the details. Demonstration of *P. punctatus* as the sister group of all other *Pyramodon* and a slope-dwelling taxon as the sister group of all carapids would help corroborate bathymetric vicariance as a relevant isolation mechanism in carapids. Peripheral isolation of *P. lindas* on the southern border of the shallow, northern form and, subsequently, of *P. parini* on the southeastern border, would produce the observed pattern. In view of our uncertainty about the relative importance of latitude and depth in the initial isolation event, it is worth pointing out that subsequent events appear to have taken place latitudinally (Fig. 114).

Echiodontini.—Several species in this tribe are represented by one or a few lots and, therefore, our discussion of their zoogeography is limited. Three broad patterns are evident in this tribe: tropical Indo-west Pacific, austral temperate and boreal temperate.

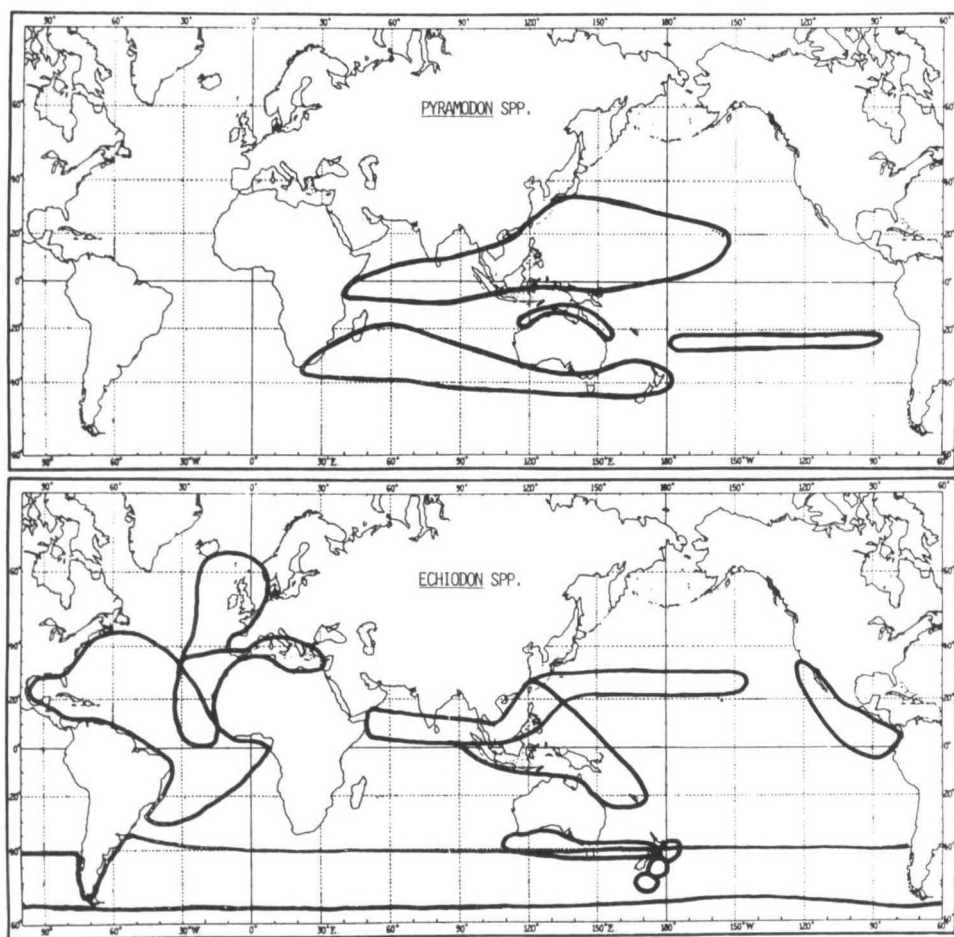


Figure 114. Generalized distribution tracks in the genera *Pyramidon* and *Echiodon*.

Eurypleuron owasianum is unusual in its disjunct, anti-equatorial distribution (see species account). If it is, in fact, more broadly distributed over the tropical and temperate Indo-west Pacific, its distribution covers all three broad patterns identified above. It would, therefore, be broadly sympatric with at least some species in its sister group, *Echiodon*. Williams (1984a) treated the northern form as a separate species. Although we do not treat the differences as specifically distinct (see species account for details), the separation of northern and southern populations is consistent with the more commonly observed carapid pattern of north-south vicariance and might be considered corroboration of Williams' conclusion. The genus, of course, retains a broadly sympatric pattern with its sister genus, *Echiodon*.

Echiodon is a diverse, enigmatic genus (Williams, 1984a). With the exception of *Ec. coheni*, it is absent from the tropical Indo-west Pacific. The distribution of *Ec. coheni*, plus those patterns seen in *Onuxodon* and *Eurypleuron*, suggests an outer shelf Indo-west Pacific distribution for the tribal ancestor. Most subsequent radiation in *Echiodon* seems to have involved peripheral isolation.

On the basis of our *Echiodon* cladogram (Fig. 45), there was initially a Tethyan

event with the *drummondi-dentatus* group becoming peripherally isolated in the North Atlantic (Fig. 114). In the other species, there are two groups that are almost completely allopatric. One group contains the rare southern Australian and New Zealand species (*pukaki*, *pegasus*, *rendahli* and *neotes*) and the other contains a largely boreal temperate/subtropical group (unnamed, *dawsoni*, *exsilium*, *coheni*) plus the austral *Ec. cryomargarites* (Figs. 66, 67, 70, 78). Again the pattern suggests north-south vicariance. It also suggests a more complicated scenario perhaps involving an initial bathymetric isolation of *Ec. cryomargarites* (it is the deepest dwelling carapid). The amphi-American species (*Ec. exsilium* and *Ec. dawsoni*) are not sister taxa according to our cladogram (Fig. 45). Our cladogram specifies that *Ec. exsilium* differentiated before a broadly distributed Indo-Pacific-Atlantic form differentiated into *Ec. dawsoni* and *Ec. unnamed*. The latter event presumably would correspond to the formation of the Panamanian isthmus, about 3.1 million years ago (Keigwin, 1978) and implicates an Indo-Pacific rather than a Tethyan origin for *Ec. dawsoni*.

Onuxodon is unique in Echiodontini since it is a shallow water form (less than 50 m) and tropical Indo-Pacific in distribution. *Eurypleuron* and most *Echiodon* are found on the outer shelf (greater than 100 m) or upper slope as deep as 1,600 m (Markle et al., 1983). The deep water distribution of its sister taxa (including the subfamily-level sister taxon, Pyramodontinae) suggests that the cladogenetic mechanism involved in the *Onuxodon*-(*Echiodon* + *Eurypleuron*) isolation event was at least partly bathymetric. The implication is that *Onuxodon*, a shallow water tropical genus, evolved from a slope-dwelling ancestor. Clearly the association of *Onuxodon* with large bivalves is a part of the adult's bathymetric requirements and may be the ecological novelty that allowed them to compete successfully in shallow water. Within the genus there are two broadly sympatric species, *O. fowleri* and *O. parvibrachium*, and one apparently allopatric form, *O. margaritiferae* (Figs. 87, 90). In contrast to the non-inquiline genera, *Onuxodon* and the inquiline carapins (*Encheliophis*, and to some degree *Carapus*) have broadly sympatric distribution patterns that are centered on Indonesia. Species in the non-inquiline genera tend to be distributed outside the tropical Indo-west Pacific, or to be in outer shelf-upper slope habitats.

Carapini.—The Carapini are almost exclusively shallow water (less than 50 m) and tropical (Figs. 95, 103, 104, and 115). Our cladogram (Fig. 46) of *Carapus* is poorly resolved, but the allopatry of *C. acus* and *C. bermudensis* from the rest of the tribe argues for an initial Tethyan vicariance of ancestral *Carapus* in the Atlantic and *Encheliophis* in the Indo-Pacific.

Interestingly, the species of *Carapus* that subsequently reinvade the Indo-Pacific are *C. mourlani* and *C. sluiteri*, both of which are non-holothurian inquilines. Since *C. acus* and *C. bermudensis* are holothurian inquilines, as are all but one *Encheliophis*, the tribal ancestor was also likely a holothurian inquiline. The non-holothurian hosts of *C. mourlani* and *C. sluiteri* could conceivably be viewed as a derived state which would resolve the trichotomy in our cladogram (Fig. 46). More importantly, it suggests that the key to establishment of sympatry between *Carapus* and *Encheliophis* was character displacement or shift of the plesiomorphic form (*Carapus*) from a holothurian to a non-holothurian host.

The species of *Encheliophis* are broadly and sympatrically distributed in the Indo-Pacific (Fig. 115). Evidence for peripheral isolation is seen in *En. sagamianus* and *En. dubius*. As is the case with *Echiodon*, the amphi-American species of Carapini are not sister taxa. *Encheliophis dubius* is an allopatric peripheral isolate of a broadly distributed ancestor of *En. homei* and is not closely related to the

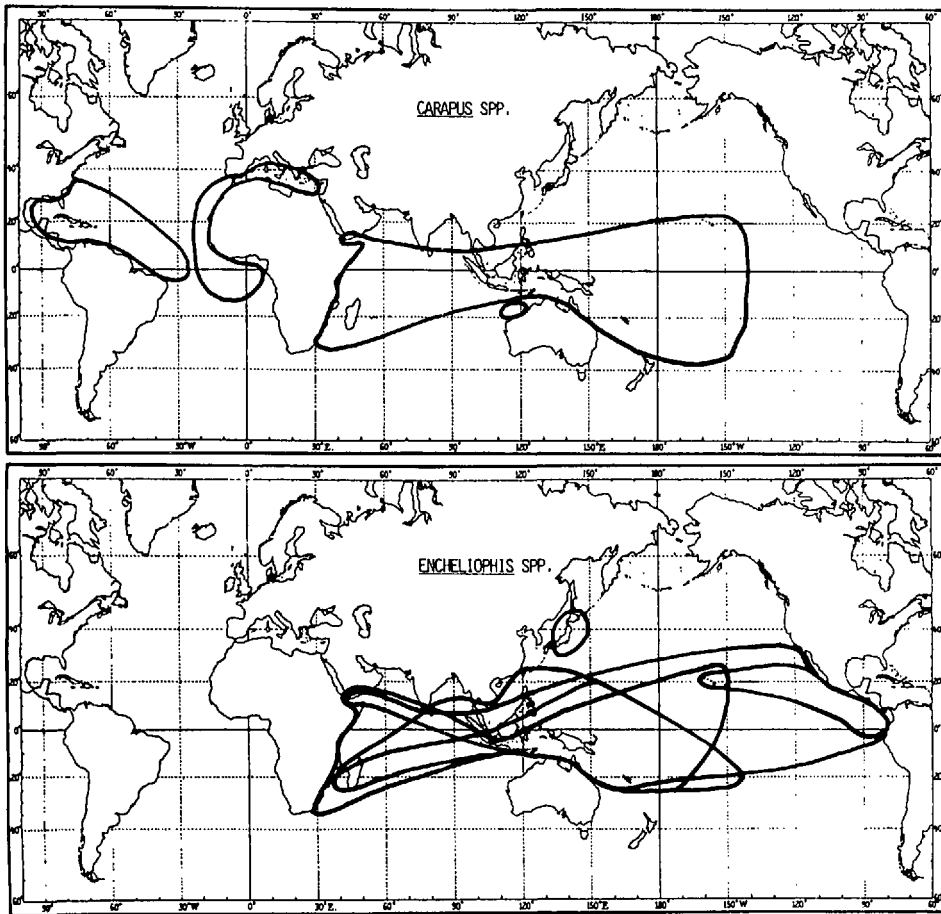


Figure 115. Generalized distribution tracks in the genera *Carapus* and *Encheliophis*.

Atlantic *C. bermudensis*. The other eastern Pacific carapid, *En. vermicularis*, has a longitudinal distribution surpassed only by *S. canina* and is remarkable for its widely disjunct populations (Fig. 105), none of which are Atlantic.

The similarity of distribution patterns in *Encheliophis* spp. (Fig. 115) might be evidence in support of some form of sympatric isolating mechanism, perhaps through changes in host specificity. However, we note complete or nearly complete allopatry in two pairs of sister species in the genus: *sagamianus-vermiops*, and *vermicularis-gracilis* (Figs. 104, 105). The greatest sympatry occurs in the latter pair, but they too show significant allopatry since *En. vermicularis* is absent from the Pacific Plate though present marginally in the east and west and *En. gracilis* is both on and off the Plate throughout the tropical Indo-west Pacific, but is absent from the eastern Pacific (Fig. 104). *Encheliophis boraborensis* is broadly distributed both on and off the Pacific Plate and throughout the tropical Indo-west Pacific as are *En. homei* and *En. gracilis*. An ancestral *Encheliophis* was probably distributed throughout the tropical Indo-west Pacific.

There is an Indian Ocean disjunction in distribution of *Encheliophis homei* (Fig. 103), *En. gracilis* (Fig. 104), *En. vermicularis*, and *En. vermiops* (Fig. 105). We are not certain if these disjunctions are real or artifacts of sampling. In those

cases in which our sample size permitted some examination of geographic variation (see *En. vermicularis*, Table 21), wide ranging taxa showed little differentiation. We attribute the lack of differentiation to the teleplanktonic larval stage. In the case of *Onuxodon parvibrachium* (Fig. 87) larval records bridge an apparent adult disjunction. However, in the case of *Carapus/Encheliophis*, larval records do not bridge the disjunction (Fig. 96) and the question remains unresolved.

Carapids and the Eastern Pacific Barrier.—Three carapids, *Echiodon exsiliun*, *Encheliophis dubius* and *En. vermicularis*, are found in the eastern Pacific and none has its closest sister taxon in the western Atlantic. As is the case with shallow water hermatypic corals, their closest phylogenetic affinities are with Indo-west Pacific taxa (Dana, 1975). Additional examples of broadly distributed Pacific taxa or of eastern Pacific-Indo-Pacific sister taxa can be found in other fishes. For example, in antennariids: *Antennatus* contains only two species, one in the Indo-Pacific and one in the eastern Pacific; the eastern Pacific *Antennarius avalonis* is part of an unresolved trichotomy with an Indo-Pacific species and a western Atlantic species pair; and two broadly distributed Indo-Pacific species, *Antennarius commersoni* and *A. coccineus*, are also found in the eastern Pacific (Pietsch and Grobecker, 1987). In the mesopelagic platytroutid genus, *Sagamichthys*, there is evidence to indicate that the eastern Pacific *S. abei* is more closely related to its Indian Ocean congener than to its Atlantic relative (Matsui and Rosenblatt, 1987). In order to account for this pattern, one is obliged to invoke one to several extinctions. Two geological events are relevant to consider: 1) the Pliocene formation of the Panamanian isthmus about 3.1 million years ago (Keigwin, 1978); and 2) the apparent elimination of all reef-building corals in the eastern Pacific during the Pleistocene, with subsequent reinvasion by Indo-west Pacific species and reestablishment of the coral reef community about 5,000 years ago (Dana, 1975). Leis (1984) noted that Dana's mass extinction scenario favored pelagic dispersal as a causative factor in explaining eastern Pacific zoogeography. Carapids, with their teleplanktonic larvae, would seem to be ideal candidates for reinvasion.

However, of the three carapids in the eastern Pacific only *Encheliophis vermicularis* fits the above scenario well. Our taxonomic conclusion of conspecificity with Indo-Pacific populations and little or no habitat or morphological divergence corroborates the hypothesis that *En. vermicularis* is a recent (perhaps as young as 5,000 yr) addition to the eastern Pacific fauna. *Encheliophis dubius* may also fit the mass extinction scenario but may be a special case. It has an unusual host for its genus (bivalve molluscs) and an unusual distribution (Hawaii-eastern Pacific and possibly China but see Comments section for this species) and presumably could represent a form that survived in place by switching to a new host or a form that survived in a refugium (Hawaii) and recently reinvaded the eastern Pacific. *Echiodon exsiliun* is an outer shelf species that, as far as we know, is not dependent on coral reef communities. According to our cladogram, it must be older than the split of *Ec. dawsoni* and *Ec. unnamed* (3 million yr) and, therefore, must have survived Pleistocene calamities in place in the eastern Pacific. The only other carapids that must have been present in the eastern Pacific before the Pleistocene cooling were sister species of *Echiodon unnamed*, *Carapus bermudensis* and *Snyderidia canina*. The former two taxa were apparently extirpated, but there is no reason to predict extinction of a deep water form such as *S. canina* based on surface cooling and sea level changes. The latter is either present in the eastern Pacific and currently undetected or the extinctions were more extensive than Dana's (1975) hypothesis would indicate.

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